

JUL 1 1952

SCIENCE
LIBRARY

B10

The
American Midland Naturalist

Founded by J. A. Nieuwland, C. S. C.

John D. Mizelle, *Editor*

•

CONTENTS

The Comparative Functional Morphology of the Pelvic Appendage in Three Genera of Cuculidae.....	Andrew J. Berger 513
A Study of the Breeding Biology of the Purple Martin (<i>Progne subis</i>)	Robert W. Allen and Margaret M. Nice 606
A Contribution to the Life History and Ecology of the Plethodontid Salamander <i>Aneides aeneus</i> (Cope and Packard).....	Robert E. Gordon 666
Vertebrate Fauna of North Carolina Coastal Islands II. Shackleford Banks	William L. Engels 702
The Genus <i>Orconectes</i> in Louisiana (Decapoda, Astacidae).....	George Henry Penn 743
Some Influences of the American Hookworm.....	James E. Ackert 749
The Phloem of <i>Heterangium americanum</i>	John W. Hall 763

EDITORIAL STAFF

JOHN D. MIZELLE	Zoology
Editor, University of Notre Dame, Notre Dame, Ind.	
EDWARD A. CHAPIN	Entomology
U. S. National Museum, Washington, D. C.	
ALBERT L. DELISLE	Plant Morphology
University of Notre Dame, Notre Dame, Ind.	
CARROLL LANE FENTON	Invertebrate Paleontology
404 Livingston Ave., New Brunswick, N. J.	
JOHN HOBART HOSKINS	Paleobotany
University of Cincinnati, Cincinnati, Ohio	
GEORGE NEVILLE JONES	Plant Taxonomy
University of Illinois, Urbana, Ill.	
REMINGTON KELLOGG	Mammalogy
U. S. National Museum, Washington, D. C.	
JEAN MYRON LINDSALE	Ornithology
Hastings Reservation, Robles del Rio, Calif.	
GEORGE WILLARD MARTIN	Mycology
State University of Iowa, Iowa City, Iowa	
HUGH M. RAUP	Plant Ecology
Harvard Forest, Harvard University, Petersham, Mass.	
KARL PATTERSON SCHMIDT	Ichthyology and Herpetology
Chicago Natural History Museum, Chicago, Ill.	
HARLEY JONES VAN CLEAVE	Invertebrate Zoology
University of Illinois, Urbana, Ill.	

NOTE: THE AMERICAN MIDLAND NATURALIST, published by the University of Notre Dame is primarily, though not exclusively, devoted to the Natural History of the Middle West. A wide selection of papers on botany, paleontology and zoology is published in bi-monthly issues, three of which make up a volume.

Authors are invited to submit carefully prepared manuscripts and requested to limit tables and illustrations as much as possible. Abstracts and reprint orders should accompany manuscripts or corrected proofs.

The following numbers are out of print: Vol. 1 (1, 4, 5, 8-12); Vol. 2 (1-3, 8, 9); Vols. 3, 4 (all numbers); Vol. 5 (1, 6-8); Vol. 6 (1, 3, 7-12); Vol. 7 (1, 6); Vol. 8 (2); Vol. 9 (2); Vol. 11 (1); Vol. 12 (12); Vol. 14 (1, 5-6); Vol. 15 (4); Vol. 16 (2); Vol. 17 (1, 2); Vol. 18 (1); Vol. 20 (1, 2); Vol. 21 (2, 3); Vol. 22 (1); Vols. 23-26 (all numbers); Vol. 27 (1); Vol. 36 (1); Vol. 37 (2, 2); Vol. 38 (1). Volume groups 1-12, 13-18 and 19-44 contain 12, 6 and 3 issues respectively. Available issues of Vols. 1-6 \$4.00, single issues 40 cents; Vol. 7 \$2.50, single issues 25 cents; Vols. 8-12 \$4.00, single issues 40 cents; Vols. 13, 14 \$2.50, single issues 50 cents; Vol. 15 \$3.00, single issues 60 cents; Vol. 16 \$4.00, single issues 75 cents; Vol. 17 \$3.50, Part I, \$2.50, single issues \$1.25. Subscription price per year \$6.00.

Inquiries concerning exchanges for specimens, journals, special volumes or duplicate books should be addressed to *The American Midland Naturalist*, Notre Dame, Indiana, where subscriptions and payments are also received. Offers should accompany requests for exchange.

Abbreviated citation: *Amer. Midl. Nat.*

The American Midland Naturalist is indexed in the INTERNATIONAL INDEX.

Entered as second-class matter at Notre Dame, Indiana. Acceptance for mailing at special rate of postage provided for in section 1103; Act of October 3, 1917, authorized on July 3, 1918.

ology

nology

hology

ology

otany

enomy

alogy

ology

ology

ology

ology

ology

the
the
deon-
up a

d to
orders

(1-3,
(1,
15
Vol.
2);
issues
l. 7
14
4.00,
tion

apli-
me.
om-

EX.

ling
117,

The American Midland Naturalist

Published Bi-Monthly by The University of Notre Dame, Notre Dame, Indiana

VOL. 47

MAY, 1952

No. 3

The Comparative Functional Morphology of the Pelvic Appendage in Three Genera of Cuculidae¹

Andrew J. Berger

Department of Anatomy, University of Michigan Medical School, Ann Arbor

CONTENTS

Introduction	514	M. peroneus brevis	545
Material and methods	514	M. gastrocnemius	546
Acknowledgments	515	M. plantaris	548
Osteology		M. flexor perforatus digiti II	548
Introduction	515	M. flexor perforatus digiti III	549
Literature	516	M. flexor perforatus digiti IV	550
The axial skeleton	517	M. flexor perforans et	
The sternum	521	perforatus digiti II	550
Hypotarsus	522	M. flexor perforans et	
Discussion	522	perforatus digiti III	551
Myology		M. flexor digitorum longus	552
Introduction	530	M. flexor hallucis longus	554
Description of pelvic muscles	530	M. popliteus	555
M. iliotrochantericus posticus	530	M. extensor hallucis longus	555
M. iliotrochantericus anticus	531	M. extensor proprius digiti III	556
M. iliacus	532	M. extensor brevis digiti IV	556
M. ambiens	532	M. abductor digiti II	557
M. sartorius	533	M. flexor hallucis brevis	557
M. iliotibialis	533	M. adductor digiti II	558
M. femorotibialis externus	534	M. lumbricalis	558
M. femorotibialis medius	535	M. abductor digiti IV	559
M. femorotibialis internus	535	M. adductor digiti IV	559
M. piriformis	536	Discussion	
M. semitendinosus	537	Review of the locomotor habits	
M. semimembranosus	538	of the three genera	559
M. biceps femoris	539	Comparison of muscle variations	
M. ischiofemoralis	539	with differences in habits and	
M. obturator internus	540	limb proportions	561
M. obturator externus	541	On the classification	
M. adductor longus et brevis	541	of the Cuculidae	567
M. tibialis anticus	542	Summary	570
M. extensor digitorum longus	543	References	573
M. peroneus longus	545	Plates	577

¹ Thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

Introduction

The purpose of this study was to ascertain osteological and myological variations among three genera of Cuculidae whose habits are markedly different. These genera were selected because they represent three subfamilies according to the current system of classification (Peters, 1940: 12-76). Peters placed these genera in subfamilies as follows: *Coccyzus*, subfamily Phaenophaeinae; *Crotophaga*, subfamily Crotophaginae; *Geococcyx*, subfamily Neomorphinae. *Coccyzus* is arboreal in its habits and *Geococcyx* is almost entirely terrestrial, whereas *Crotophaga* is intermediate, inhabiting both the ground and low trees and bushes.

Many comparative anatomists of the nineteenth century directed their attention to a study of the anatomy of birds (Beddard, Fürbringer, Gadow, Garrod, Huxley, Mivart, Owen, Parker). Advances in embryology with the resultant promulgation of the recapitulation theory plus the accumulation of paleontological evidence and the appearance of the doctrine of evolution stimulated interest in the discovery of the relationships among birds, and led to attempts to classify them in the light of newly gained information. The main aim of these investigations was to establish a genetic system of classification. Most of these studies were general and descriptive in nature, however, and frequently broad conclusions were drawn from a study of only a few representatives of a family or an order. The earlier descriptions of structural differences were vague. Few measurements of skeletal elements were made, or at least published, and detailed comparative studies of skeletal and myological features of closely related forms were rare.

Within the past quarter of a century the avian anatomist has turned his attention to the functional anatomy of birds. This approach had its inception in Germany (Böker, Stolpe, Steinbacher) but was soon adopted in this country (Burt, Engels, Fisher, Miller, Richardson). Comparative study of related forms yields evidence concerning the degree of relationship and in some cases enables one to infer the nature of the ancestral type and the adaptations which have accompanied the divergence of existing forms.

In his excellent paper on the muscles of the pelvic appendage of birds, Hudson (1937) reviewed the major works pertaining to the myology of the leg which had been published to that date. It is interesting to note that no major work on avian myology appeared in America between 1890 (Shufeldt) and 1930 (Burt). Since the publication of Hudson's paper, the following additional papers have appeared in America: Miller (1937), Howell (1938) Richardson (1942), Chamberlain (1943), Fisher (1946), Wilcox (1948) and Hudson (1948).

Material and Methods

Twelve preserved specimens of the Black-billed Cuckoo (*Coccyzus erythrophthalmus*), four specimens of the Yellow-billed Cuckoo (*Coccyzus americanus*), four specimens of the Groove-billed Ani (*Crotophaga sulcirostris*), and four specimens of the Road-runner (*Geococcyx californianus*) were used in this study. In addition, the following birds were dissected in order to make

comparisons with the cuckoos: one Green Heron (*Butorides virescens*), four Ring-necked Pheasants (*Phasianus colchicus*) (tarsometatarsus and digits only), one Great Horned Owl (*Bubo virginianus*), and one Eastern Crow (*Corvus brachyrhynchos*).

Specimens were injected either with a solution of one part 100 per cent formalin to eight parts of water or with embalming fluid (3% phenol, 2% formalin, 20% glycerine, 75% water). Prolonged immersion in the embalming fluid resulted in some decalcification, but not enough to interfere with the dissections. In the dissection of the cuckoos and anis the assistance of a binocular dissecting scope with seven and ten power lenses was necessary. The smaller muscles and the insertions of the extensors and flexors of the digits in *Geococcyx* also were checked with these lenses.

The following skeletal material was used in determining skeletal relationships in the three genera: 59 specimens of *Coccyzus a. americanus*, 5 of *C. a. occidentalis*, 14 of *C. erythrophthalmus*, 6 of *Crotophaga sulcirostris*, and 25 of *Geococcyx californianus*.

ACKNOWLEDGMENTS

The writer wishes to express his appreciation to Dr. E. Raymond Hall, Museum of Natural History, University of Kansas, and to Dr. Josselyn Van Tyne, Museum of Zoology, University of Michigan, for the loan of the skeletal material used in this study.

Specimens of the road-runner were obtained through the courtesy of Mr. W. C. Glazener, Director of the Game, Fish and Oyster Commission, Austin, Texas. Special thanks are due to Mr. P. B. Uzzell of the Commission for collecting and shipping the specimens. The anis were obtained through the generosity of Dr. George M. Sutton, who collected them for me on his 1949 expedition to Mexico. I am indebted to many colleagues at the University of Michigan who kept me supplied with specimens of both the Yellow-billed and Black-billed Cuckoos.

The author is especially indebted to Dr. Alfred H. Stockard under whose direction this investigation was made. His encyclopedic grasp of the fundamentals of comparative anatomy and his judicious guidance continually encouraged the writer to persevere in the completion of sometimes tedious aspects of the study.

Osteology

INTRODUCTION

An analysis of the skeletal elements of the vertebral column and appendages of the three genera of cuckoos was made. Non-pelvic elements were included in order to interpret differences in the skeleton and musculature of the pelvic appendage, and in order to correlate its bony and muscular structure with the habits of the several species under consideration. A knowledge of the amount of variation within the several regions of the vertebral column was desired in order to determine what element in it might be used as a satisfactory standard to which the limb elements could be compared.

Although the primary objective of this study was to analyze the pelvic appendage, it seemed essential also to consider osteologically the pectoral appendage in order adequately to interpret differences in proportions of the leg in the three genera. This portion of the osteological study is in most respects a repetition of the work of Engels (1938), although his study was

based on only a few specimens: three skeletons of *Coccyzus a. americanus*, two of *Crotophaga sulcirostris* and nine of *Geococcyx californianus*. It is true, as Engels states, that this small number is adequate for such a study because the extremes in locomotion between *Coccyzus* and *Geococcyx* are clearly reflected in skeletal proportions. Nevertheless, certain aspects of the problem were not covered by Engels and discussing these necessitated a re-investigation involving a larger number of specimens. A study of the Black-billed Cuckoo also seemed pertinent.

In the interest of standardization, measurements were made after Larson (1930), except for "depth of carina" and "total length of scapula." Depth of carina was taken at the midpoint of the longitudinal axis of the keel; no precise dorsal limit for this depth was evident on the bone. The only consistent results in measuring the length of scapula were obtained by placing the bone on the table and slowly closing the jaws of the calipers until the scapula could be raised from the table. It was often difficult to ascertain if the tip of the scapula had been broken; doubtful specimens were discarded. In addition, considerable warping was found in the scapula and furcula. Hence, depth of carina and length of scapula and furcula are the least reliable of the measurements made.

Measurements were made with vernier calipers accurate to one tenth of a millimeter.

The nomenclature of Howard (1929) was used for skeletal parts, except that my "external condyle" equals both the "fibular condyle" and "external condyle" of Howard. In addition, I have adopted the term "fovea iliaca anterior" as employed by Newton (1896: 861).

Synonymy for skeletal elements is relatively simple. It seemed advisable, however, to review the literature for synonymy of the hypotarsus.

The anteroventral surface of the ilium of the three genera bears a conspicuous lateral process. Because of the importance of this process in the origin of certain muscles I have named it the *anterior iliac process*. It was not found to be developed in several other families examined (Anatidae, Picidae, Corvidae, Ploceidae) but a small lateral process was found in Falconidae.

LITERATURE

A number of authors have dealt with the osteology of the Cuculiformes. Huxley's paper (1867) was the stimulus for much of the later work, particularly on the skull. In this paper (p. 444) he discussed briefly the skull of *Cuculus canorus*, *Geococcyx* and *Phaenicophaeus*. Parker (1876: 120-122) described the skull of *Scythrops novae-hollandiae*. Shufeldt (1884) compared the skull in *Geococcyx* and *Coccyzus americanus*; and in 1886 he described and figured the entire skeleton of *Geococcyx*. In 1901 Shufeldt published on the osteology of *Geococcyx*, *Crotophaga* and *Coccyzus americanus*, but failed to label plates or give measurements, and treated the pectoral and pelvic limbs in only a very general manner. Beddard (1898a) described the anatomy of *Scythrops novae-hollandiae*, and in 1901 presented an excellent account of the

anatomy of *Carpococcyx radiatus* and included a series of measurements of the leg bones of *Geococcyx*. The most complete comparative study of the Cuculiformes was presented by Pycraft (1903). Apparently, however, he lacked material of *Coccyzus*, and had little to say about it. Shufeldt (1909) repeated much of his earlier work on *Coccyzus*, *Crotophaga* and *Geococcyx* in comparison with *Coccytes glandarius*, but confined his measurements of the humerus, ulna, carpometacarpus and index digit to the latter species and *Cuculus canorus*. In attempting to determine the systematic position of the road-runner of the middle and late Pleistocene, Larson (1930) tabulated measurements of the bones of both Recent and Pleistocene material and illustrated the method of taking measurements. This paper was followed by that of Engels (1938) who presented graphically the limb proportions of *Geococcyx*, *Crotophaga* and *Coccyzus americanus*.

THE AXIAL SKELETON

Along with the analysis of the axial skeleton, referred to above, I have attempted to consolidate data on the Cuculidae from all available sources. Definitions pertaining to avian anatomy are widely scattered, and those considered pertinent have been added to this paper.

Cervical vertebrae.—Beddard (1898b: 112) defined the cervical vertebrae as follows: "It is customary to regard as cervical those vertebrae which either have no movable ribs or, if they have, do not become connected through their intermediary with the sternum." Newton (1896: 848) stated that the cervical vertebrae are "all those that lie between the SKULL and the first vertebra which is connected with the sternum by a pair of complete ribs; but they may be subdivided into (a) Cervical vertebrae, in the strict sense—either without rudimentary ribs, as the Atlas, or having rudimentary ribs which are fused with the vertebra; and (b) Cervico-dorsal vertebrae, with movable ribs which do not reach the sternum." The last two definitions, as might be expected, are the ones used by Gadow and Selenka (1891: 947), who stated that they were first so used by Fürbringer (1888: 106). Pycraft (1903: 272) replaced "cervico-dorsal" by "cervico-thoracic," stating that "The cervico-thoracic vertebrae may be two or three in number. The number of true cervicals varies, being either 11 or 12." I have adopted the definition of cervical vertebrae as given by Newton.

Other references concerning the number of cervical vertebrae in the Cuculidae follows: Fürbringer (1888: 779) gave 13 as the number for *Crotophaga* and 14 for *Cuculus* and *Centropus*. Gadow and Selenka (1891: 950) gave 14 cervical vertebrae as the number for the Cuculidae, and (1893: 213) 14 or 15 for the Cuculi. In 1892 (p. 249) Gadow listed 14 for the Cuculidae. Beddard (1898b: 279) said: "No cuckoo has more than 14 cervical vertebrae, and some have only 13," but did not give examples of the latter. Shufeldt (1901 and 1909) stated that *Geococcyx*, *Crotophaga*, and *Coccyzus* possess 14 cervical vertebrae each. Steinbacher (1935: 255) gave 14 for the Cuculidae.

In each of the complete skeletons of *Geococcyx californianus* and *Croto-*

phaga sulcirostris examined by me there were 14 cervical vertebrae. In the genus *Coccyzus*, however, I found only 13 cervical vertebrae. The number of articulated skeletons available for this determination was: *Coccyzus a. americanus*, 12; *C. a. occidentalis*, 3; *C. erythrophthalmus*, 6.

Cervicodorsal vertebrae.—According to Shufeldt (1901 and 1909) there are two cervical vertebrae bearing movable ribs in *Geococcyx* and *Crotophaga*. This agrees with my findings. In *Coccyzus*, however, he stated that there are three pairs of cervical ribs. I find only two pairs in this genus. The first of these ribs is about one half the length of the second, so that if a third exists anteriorly it must be quite rudimentary and easily lost or destroyed in the preparation of the specimens. Coues (1903: 144) said, regarding the cervicodorsal vertebrae: "The rule is two such free pleurapophyses or cervical ribs of any considerable length; sometimes one; rarely three; in the cassowary four."

In all three genera the last pair of cervical ribs always bears an epipleural process (Shufeldt, 1886a: 252). or uncinat process (Coues, 1903: 148). In one specimen of *Crotophaga sulcirostris* (K.U. No. 23609) and one specimen of *Geococcyx californianus* (K.U. No. 20363) both of the cervical ribs bear these processes.

In one specimen of *Geococcyx* (K.U. No. 20363) the 14th (last) cervical vertebra possesses a pair of ribs which articulate with a pair of sternal ribs. According to the definition given in the following paragraph this vertebra should be classified as dorsal rather than cervical. However, the articulation of the sternal rib with the sternum is abnormal and, therefore, it should be called a cervical vertebra (see Lucas, 1888, 1889 and 1893; Shufeldt, 1888).

Dorsal vertebrae.—Huxley (1872: 237) stated: "The first dorsal vertebra is defined as such, by the union of its ribs with the sternum by means of a sternal rib; which not only, as in the *Crocodylia*, becomes articulated with the vertebral rib, but is converted into complete bone, and is connected by a true articulation with the margin of the sternum." Newton (1896: 849) said: "*Dorsal vertebrae* begin at the first that is connected with the sternum by a pair of complete ribs, and end at the last that is not fused with the ilium." He distinguished between dorsal and thoracic vertebrae. The latter are fused to the synsacrum although they may have ribs reaching the sternum. All of the species under consideration possess four dorsal vertebrae, which are free and are not fused to form a notarium (Böker, 1935: 103; Adams, 1938: 110).

Synsacrum.—Some investigators have attempted to identify the synsacral vertebrae by tracing spinal nerves. This technique has led to different interpretations, apparently because of individual variation in the lumbosacral plexus (Boas, 1933). The ultimate determination probably is dependent upon comparative embryological studies. It is not surprising, therefore, to find little agreement among authors upon the terminology for or the number of fused vertebrae composing the synsacrum. For example, many authors state that there are two true sacral vertebrae, as in the reptiles, involved in its formation: Gegenbaur, 1878: 435; Pycraft, 1903: 273; Wiedersheim, 1909: 72; Gadow, 1933: 313. Zittel (1932: 429) defined these as follows: "The true sacra are those two lying behind the cavity containing the kidneys, having

transverse processes, and sacral ribs reaching from their centra to the ilia. The rib-like nautre (*sic*) of these processes may be seen in embryos, particularly of the ostrich, which as well as apteryx has 3 sacra's." Mivart (1879: 328) in speaking of the Pelecanidae said that "there are three sacral vertebrae—the Thirtieth, Thirty-First and Thirty-Second." Beddard (1898b: 112) pointed out that in *Apteryx* and the ostrich there are three sacral vertebrae, and in *Larus* and *Chionis* there is "apparently only one sacral vertebra." Coues (1903: 147) stated that there may be three, four, or five true sacral vertebrae. There is similar disagreement concerning the identification of the other vertebrae composing the synsacrum, which may be due primarily to variation between genera or even within a single species.

Regarding the total number of vertebrae in the synsacrum, and with special reference to the cuckoos, Pycraft (1903: 273) stated that there are eleven fused vertebrae in the synsacrum of *Geococcyx* and *Crotophaga*. Shufeldt (1901: 18 and 46) reported eleven for *Geococcyx* and a young *Coccyzus americanus*. Larson (1930: 413) also reported eleven (2 thoracic, 3 lumbar, 2 lumbosacral, 2 sacral and 2 caudal) in *Geococcyx*.

Even though it has not been possible to classify satisfactorily the vertebrae in the synsacrum, a reasonably accurate estimate of the total number in it can be made by counting its nerve foramina and transverse processes. Table I summarizes my determinations by this method.

TABLE I.—Number of fused vertebrae in synsacrum

No. of fused vertebrae	Number of specimens			Geococcyx	
		Coccyzus	Crotophaga		
	amer.	occident.	erythrop.		
11	15	1	3	4	22
12	40	4	10	2	2
13	2	—	—	—	—

This variation in the number of vertebrae among specimens of unknown ages is not surprising, since the synsacrum is formed by the gradual fusion of individual vertebrae during ontogeny. Notwithstanding this variation, there is a preponderance of 12 in the genus *Coccyzus* and 11 in *Crotophaga* and *Geococcyx*. Storer (1945: 443) reported variation in the number of fused vertebrae in the Alcedidae stating that "the average number of fused vertebrae in the different forms is significant."

There appears to be no significant correlation between the number of fused vertebrae in the synsacrum and the number of free caudal vertebrae.

Free caudal vertebrae.—The number of free caudal vertebrae (i.e., those between the synsacrum and the pygostyle) can be told precisely in articulated skeletons. For Cuculiformes Pycraft (1903) reported 6 or 7 free caudal vertebrae. Shufeldt gave for *Geococcyx* (1886), *Crotophaga* (1901), and *Coccyzus* (1909) 5 each, and Larson (1930) gave 5 free caudals for *Geococcyx*.

I find the number of free caudal vertebrae to be not as constant, however, as these authors state. Table II summarizes my counts.

TABLE II.—Number of free caudal vertebrae

No. of free caudals	Number of specimens				
	Coccyzus			Crotophaga	Geococcyx
	amer.	occident.	erythrop.		
4	—	—	—	2	—
5	39	5	11	3	20
6	18	—	3	1	2

Burt (1930: 477) said of woodpeckers that "the number of free caudals varies with age and the amount of fusion that has taken place. In the younger specimens the number of free vertebrae is naturally greater than in mature individuals." Although this greater fusion in older individuals is what one would expect, I am unable to make this statement regarding the cuckoos since I had no data on the age of the specimens.

In addition to the variation in the number of free caudal vertebrae, several specimens exhibited varying degrees of fusion of additional vertebrae with the pygostyle. Such fusion was observed in 6 *Coccyzus a. americanus*, 1 *C. a. occidentalis*, 2 *Crotophaga sulcirostris* and 2 *Geococcyx californianus* (see Plate XIV). Richardson (1942: 328) found a similar condition in *Dendrocolaptes* and *Glyphorhynchus*.

Pygostyle.—The posterior caudal vertebrae fuse to form a pygostyle which serves as the support for the rectrices. The number of vertebrae so fused must be determined embryologically. Few such studies have been made and authors differ as to the numbers of vertebrae involved among the several orders of birds. Gegenbaur (1878: 435) stated that the pygostyle is composed of from four to six caudal vertebrae "which were separate in the embryo." Gadow (1933: 315-316) said that "the latter [pygostyle] is composed, as ontogeny shows, of six to seven vertebrae." Parker and Haswell (1947, vol. 2: 434) stated that it is formed by the "fusion of four or more of the hindmost caudal vertebrae." Burt (1930) stated that there are six in *Colaptes auratus luteus*. Pycraft (1903: 273) said that in the Cuculi "the last two caudal vertebrae combine to form a well-marked *planum anale*."

There is another aspect of the structure of the pygostyle which should be mentioned. Huxley (1872: 239), in speaking of the pygostyle, said that it "supports the tail-feathers and the uropygial gland, and sometimes, as in the woodpeckers and many other birds, expands below into a broad polygonal disk." Richardson (1942: 325) presented data on the length, height and width of the pygostyle in certain tree-trunk foraging birds, the width being that of the disc. He stated that "the size of the disc of the pygostyle is determined chiefly by the strength of the depressor muscles which insert on the ventral

and lateral margins of the disc. Outlines of the pygostyles (fig. 5) show that birds which use the tail for support have a relatively large disc." I found no reference to this disc in the literature on the cuckoos.

Although absent in *Geococcyx* and *Crotophaga*, a disc is well-developed in the arboreal *Coccyzus*. The advantage of a disc for the support of the stiff tail feathers in tree-trunk foraging birds is readily seen. The explanation for this disc in *Coccyzus* seems more remote. The cuckoo frequents thickets and the understory of woods. It is not a strong flyer although its migration covers considerable distances. When alarmed, both captive and wild Yellow-billed Cuckoos move the tail up and down repeatedly in an irregular cadence. This use of the tail as an expression of internal "emotions," however, is no more pronounced than in many passerine birds, for example, the Cardinal (*Richmondia cardinalis*). Nevertheless, there seems to be little doubt that the development of the disc in *Coccyzus* is directly correlated with the development of *M. piriformis pars caudofemoralis*. The conclusion, therefore, appears to be that the greater development of this muscle and the disc on the pygostyle in *Coccyzus* is correlated with the greater use of the tail as a rudder in flight. Table III indicates the development of the disc.

TABLE III.—Measurements of the disc on pygostyle

Species	No. of specimens	Mean height	No. of specimens	Mean width of disc
<i>C. a. americanus</i>	50	10.39	47	3.98
<i>C. a. occidentalis</i>	5	10.52	5	3.96
<i>C. erythrophthalmus</i>	12	9.97	12	3.84
<i>C. sulcirostris</i>	5	11.46	5	2.10
<i>G. californianus</i>	22	23.12	23	2.77

THE STERNUM

The structure of the sternum in the Cuculiformes was treated in detail by Pycraft (1903), and that in the three genera now under consideration was treated by Shufeldt (1901). Although both authors commented on variation in the depth of the keel, neither presented measurements of this structure or of the total length of the sternum. Since the depth of the carina is an indicator of the development of the pectoral muscles and, hence, is correlated

TABLE IV.—Length of sternum and depth of carina

Species	No. of Bones	Mean length of sternum	No. of bones	Mean depth of carina	Ratio
<i>C. a. americanus</i>	52	23.6 ± .14	54	7.1 ± .07	3.32:1
<i>C. a. occidentalis</i>	4	23.9 ± .11	4	7.7 ± .45	3.10:1
<i>C. erythrophthalmus</i>	10	22.1 ± .32	12	6.9 ± .25	3.20:1
<i>C. sulcirostris</i>	6	23.9 ± .55	6	6.9 ± .20	3.46:1
<i>G. californianus</i>	20	35.6 ± .54	20	6.9 ± .14	5.17:1

with flying ability, these data are of particular significance. Table IV reveals the shallow nature of the carina of the cursorial road-runner in contrast with its depth in the other more arboreal genera.

HYPOTARSUS

Located on the posterior aspect of the proximal end of the tarsometatarsus there is a process for the passage of the flexor tendons to the digits. This process differs in its formation in different orders of birds. It may take the form of a single wide groove (Falconiformes), or several grooves (Anseriformes) or the grooves may be arched over to form one or more bony canals (Cuculiformes, Passeriformes).

During the past ninety years there has been considerable discussion concerning the origin of and consequently the terminology for this process. Much of the discussion has centered around the possibility that this process is homologous with the os calcis of other vertebrates. The homology has not yet been determined, but it seems desirable to list the synonymy for it and to adopt one term for its designation.

Since the term "calcaneal process" implies homology with the calcaneum, I have adopted "hypotarsus" to designate this process. I believe that the term hypotarsus was introduced by Huxley. It has been possible to trace the use of the term back to Huxley (1868: 296) who stated: "The hypotarsus (commonly called the calcaneal process) of the tarsometatarsus is traversed by a single canal."

Terms applied to this process by various authors follow: *Calcaneal process*, Owen (1866: 80; 1879: 200), Shufeldt (1881: 619); *Tendinous process*, Shufeldt (1883: 697); *Os calcis*, Coues (1866: 160), Wilcox (1948: 10); *Perforated process*, Hudson (1937: 35); *Hypotarsus*, Huxley (1868: 296), Marsh (1880: 95), Shufeldt (1884: 294), Fürbringer (1888: 1050), Gadow (1892: 255).

DISCUSSION

Several authors have analyzed the appendages of related species in an attempt to ascertain what changes have occurred in their elements in the development of cursorial birds from a supposed arboreal ancestor. They have further computed ratios between wing and leg segments to determine if an increase in leg length is accompanied by a corresponding decrease in wing length (Böker, 1927, 1935; Larson, 1930; Engels, 1938, 1940). Marples (1930) studied changes in proportions in the wing bones during development and studied the proportions in the skeleton of adult birds of different species. Beebe et al. (1917, chapter 19) reported on the growth of the several elements of the appendages of *Crotophaga ani* during embryonic development. Engels (1940) pointed out that it is possible to determine the amount of change which has taken place in the length of each segment independently of the remaining segments only by computing ratios of the dimensions of the several individual segments of the appendages against the dimensions of some standard element outside of the appendages themselves.

It has been assumed that the vertebral column is more stable in evolution

than are the paired appendages. In his study of the American thrashers, Engels (1940: 367) compared with each other the ratios of limb-segment lengths to each of the following two sections of the vertebral column: (1) Trunk length, "taken along the middorsal line from the level of a plane passing through the two acetabulae, perpendicular to the vertebral column, to the anterior end of the neural spine of the last vertebra bearing a free rib," (This measurement, to the nearest millimeter, was made with a flexible steel tape.), and (2) Thoracic length, "taken between the anterior articulating surface of the centrum of the 14th (last cervical) and the posterior articulating surface of the centrum of the 19th (last free thoracic) vertebra, in the midline." (This measurement was made with dial type calipers.) In computing ratios of wing elements, Böker (1927) used a "Rumpflänge" measurement, which is the length of the body exclusive of neck and tail and was made from approximately the center of the glenoid fossa to the center of the acetabulum.

The landmarks for measurement of trunk length used by both Engels and Böker are of doubtful value. It is difficult to locate the center of the acetabulum or glenoid fossa with either a steel tape or calipers. Neural spines are frequently broken. Furthermore, prepared, articulated avian skeletons are difficult to obtain in significant numbers and disarticulated skeletons yield unreliable information. Disarticulated vertebrae must be strung on a rigid rod in order to measure them. The ideal "standard" for computing ratios would be a single, sturdy element which would be well preserved and therefore suitable for accurate measurement. For this reason, measurements of the length of two different portions of the axial skeleton—cranium and synsacrum—in addition to length of the thoracic complex were made.

Length of cranium—from the posteriormost portion of the skull to the nasofrontal hinge. It has been shown that the bill is readily subject to adaptation (Engels, 1940; Burt, 1930), but my measurements show the cranium to be relatively stable. With the exception of those on *Geococcyx* biometric computations (see Tables V-VIII) reveal less variation in this region than in the other two regions used. The writer doubts, however, whether the anterior limit for measurement (the nasofrontal hinge) can be determined accurately in adult specimens where fusion of the cranial elements is complete.

Total length of synsacrum—from the anterior face of the first to the posterior face of the last fused centrum of the synsacrum. There is no doubt concerning the degree of accuracy with which this measurement can be made. The synsacrum possesses the advantage of being least often damaged during collection or preparation so that the measurement can be made in nearly all skeletons. Data presented above (page 519) reveal the extent of variation in the number of fused vertebrae composing the synsacrum, and tables V-VIII show its length to be more variable than is either the length of cranium or the length of the dorsal region. This measurement was abandoned, therefore, in the computations of ratios of limb segments.

Length of dorsal region—the measurement used by Engels (1938, 1940) and Richardson (1942) under the name of Thoracic length (i.e., from the

anterior articulating surface of the last cervical to the posterior articulating surface of the centrum of the last dorsal vertebra). Because of the lack of reliability of the measurements for cranial length and the greater variability in total length of synsacrum, I have used the length of the dorsal region as the standard with which to compare other skeletal elements.

Histograms showing the ratios of the lengths of the limb segments to that of the dorsal region have been prepared. Chart I illustrates differences in length of leg segments in terms of dorsal region. From the data presented in this paper it can be shown that there is a relative as well as an absolute increase in length of each segment of the leg in *Geococcyx* over *Coccyzus erythrophthalmus*, and that this increase is progressive distad, except in digit III. To illustrate: the femur, tibiotarsus and tarsometatarsus of *Geococcyx* show a 28.2, a 44.5 and a 58.4 per cent increase over the corresponding bones of *Coccyzus*, while digit III shows only a 16 per cent increase. If we omit consideration of digit III, which Engels likewise omitted, these data substantiate his conclusions (1938: 207) that "the direct adaptation to the cursorial habit in terrestrial birds lies in further elongation of the whole leg, the distal segments undergoing a relatively greater elongation than the femur; the greatest degree of elongation is shown by the most distal element." The leg segments of *Crotophaga*, also, are longer than those of *Coccyzus*, but the proportional differences are not the same as those between *Coccyzus* and *Geococcyx*. The femur, tibiotarsus, tarsometatarsus and digit III of *Crotophaga* show a 1.4, a 15.0, a 14.6 and a 2.4 per cent increase, respectively, over the corresponding bones in *Coccyzus erythrophthalmus*. These data are considered to be indicative only because of the few specimens of *Crotophaga* available for measurement.

Chart II illustrates ratios of lengths of wing segments to dorsal region. Engels (1938: 214) stated that in the wing "there is a progressive reduction in the length of each segment, including the humerus, and therefore of the whole wing in relation to the body . . . all segments of the wing are reduced in *Geococcyx* as compared to *Coccyzus*, but the reduction is greatest in the manus, less in the ulna, and least in the humerus." The data presented here support Engel's statement only with respect to the manus. The manus does show a progressive decrease as we pass from *Coccyzus* to *Crotophaga* to *Geococcyx*: *Crotophaga* shows a 12.9 per cent decrease from *Coccyzus*, and *Geococcyx* shows a 17.6 per cent decrease from *Coccyzus*. On the other hand, these data show a 1.3 per cent increase in the ratio for the humeral length in *Geococcyx* over that in *Coccyzus erythrophthalmus*; and with respect to the ulna, *Crotophaga* exhibits a greater decrease (17.1%) from *Coccyzus* than does *Geococcyx* (10.0%).

These relationships of all elements of the appendages to each other and to the length of the dorsal region can best be shown by adopting Böker's "bildlichen Indizes" (1927). One hundred is used here to represent length of the dorsal region and each element is reduced to its corresponding ratio. Chart III illustrates the superimposed bildlichen Indizes for the three genera. By this means it is possible at a glance to discern the relationship of wing and leg segments. Chart IV, using the several limb segments of *Coccyzus*

erythrophthalmus as standard, is introduced to illustrate the progressive decrease in wing segments and the progressive increase in leg segments distad in *Geococcyx* over *Coccyzus*, and to demonstrate the lack of conformity to this pattern in *Crotophaga*. Inspection of these figures reveals that Engel's results are corroborated with respect to the relative increase in the elements of the pelvic appendage, but the concomitant decrease in the elements of the pectoral appendage holds true for the manus only. Each element in the wing of

TABLE V.—Measurements in millimeters of certain bones of *Coccyzus a. americanus*

Measurements	No. of elements	Minimum	Maximum	Mean	Standard deviation	Coef. var.
Dorsal region	56	18.8	22.0	20.5 ± .09	.72	3.53
Cranium	53	22.0	24.5	23.0 ± .08	.59	2.56
Synsacrum	53	21.4	27.5	24.4 ± .18	1.34	5.49
Femur	94	26.4	29.8	28.0 ± .08	.74	2.64
Tibiotarsus	95	37.6	42.0	39.8 ± .10	1.01	2.54
Tarsometatarsus	108	24.5	28.6	26.2 ± .08	.82	3.12
Digit III	24	23.8	26.6	24.9 ± .15	.72	2.88
Humerus	100	27.9	32.3	29.6 ± .08	.82	2.77
Radius	103	25.3	28.6	26.7 ± .07	.71	2.67
Ulna	90	27.5	31.1	28.9 ± .08	.78	2.69
Carpometacarpus	104	14.6	16.6	15.6 ± .04	.41	2.62
Phalanx 1, dig. II	107	7.6	9.0	8.4 ± .03	.26	3.16
Phalanx 2, dig. II	82	5.6	7.0	6.4 ± .03	.25	3.92
Furcula	39	20.5	23.7	22.0 ± .11	.69	3.14
Coracoid	92	21.1	24.5	22.3 ± .07	.63	2.81
Scapula	91	22.2	28.3	26.5 ± .11	1.06	3.99
Length of Sternum	52	21.8	26.2	23.6 ± .14	.99	4.19
Depth of carina	54	5.9	8.2	7.1 ± .08	.58	8.10

TABLE VI.—Measurements in millimeters of certain bones of *Coccyzus erythrophthalmus*

Measurements	No. of elements	Minimum	Maximum	Mean	Standard deviation	Coef. var.
Dorsal region	10	18.0	20.1	19.1 ± .19	.59	3.13
Cranium	12	21.1	22.5	21.7 ± .15	.52	2.39
Synsacrum	13	21.4	24.6	22.9 ± .29	1.07	4.67
Femur	21	24.5	27.8	26.4 ± .22	.99	3.79
Tibiotarsus	19	34.4	38.9	36.9 ± .29	1.29	3.50
Tarsometatarsus	20	23.0	26.4	24.8 ± .21	.95	3.84
Digit III	8	22.1	25.7	23.8 ± .53	1.40	5.89
Humerus	28	26.5	28.9	27.9 ± .15	.81	2.89
Radius	25	22.9	26.0	24.7 ± .16	.78	3.16
Ulna	25	25.2	28.2	26.8 ± .16	.79	2.96
Carpometacarpus	24	13.6	15.3	14.6 ± .09	.49	3.35
Phalanx 1, dig. II	25	6.9	8.3	7.7 ± .08	.39	5.03
Phalanx 2, dig. II	22	5.2	6.4	5.8 ± .07	.33	5.69
Furcula	12	19.6	22.0	20.6 ± .24	.83	4.01
Coracoid	24	19.7	22.0	21.1 ± .14	.67	3.19
Scapula	21	23.2	27.5	24.7 ± .24	1.08	4.38
Length of Sternum	10	20.5	23.5	22.1 ± .32	1.02	4.65
Depth of carina	12	5.1	8.0	6.9 ± .25	.87	12.56

Crotophaga shows a decrease over *Coccyzus* but the decrease is not progressive as we move distad.

By comparing the actual length of the pectoral with that of the pelvic appendage, we see that the wing is 75, 74, 59 and 49 per cent the length of the leg in *Coccyzus americanus*, *C. erythrophthalmus*, *Crotophaga sulcirostris*, and *Geococcyx californianus*, respectively.

TABLE VII.—Measurements in millimeters of certain bones of *Crotophaga sulcirostris*

Measurements	No. of elements	Minimum	Maximum	Mean	Standard deviation	Coef. var.
Dorsal region	6	23.8	25.8	24.5 ± .34	.82	3.37
Cranium	5	26.1	27.3	26.8 ± .23	.52	1.94
Synsacrum	6	25.0	29.1	26.4 ± .67	1.64	6.24
Femur	8	33.0	35.8	34.4 ± .39	1.12	3.26
Tibiotarsus	8	51.9	55.8	54.3 ± .57	1.59	2.95
Tarsometatarsus	10	34.1	37.9	36.6 ± .40	1.28	3.49
Digit III	9	29.8	33.0	31.4 ± .39	1.18	3.75
Humerus	11	32.2	35.2	33.5 ± .29	.99	2.96
Radius	12	24.6	26.7	25.9 ± .24	.81	3.15
Ulna	11	27.2	29.3	28.4 ± .24	.79	2.77
Carpometacarpus	11	15.6	17.4	16.8 ± .17	.56	3.30
Phalanx 1, dig. II	12	7.6	8.3	8.1 ± .61	.21	2.62
Phalanx 2, dig. II	11	6.1	6.8	6.4 ± .79	.26	4.09
Furcula	4	22.5	25.3	23.9 ± .68	1.33	5.57
Coracoid	12	22.1	30.2	25.2 ± .82	2.83	11.30
Scapula	11	27.6	30.8	28.8 ± .31	1.01	3.51
Length of sternum	6	22.0	25.7	23.9 ± .55	1.35	5.67
Depth of carina	6	6.6	7.7	6.9 ± .20	.49	7.10

TABLE VIII.—Measurements in millimeters of certain bones of *Geococcyx californianus*

Measurements	No. of elements	Minimum	Maximum	Mean	Standard deviation	Coef. var.
Dorsal region	11	29.2	31.8	30.5 ± .26	.86	2.83
Cranium	21	30.7	37.5	35.6 ± .35	1.61	4.52
Synsacrum	24	37.0	45.7	40.5 ± .41	2.03	5.01
Femur	41	48.4	58.8	53.9 ± .37	2.38	4.42
Tibiotarsus	36	74.6	92.2	85.0 ± .63	3.79	4.45
Tarsometatarsus	40	57.0	67.7	62.7 ± .42	2.68	4.23
Digit III	17	40.6	48.8	44.2 ± .58	2.38	5.33
Humerus	44	42.3	49.6	45.1 ± .29	1.95	4.32
Radius	43	31.6	39.0	35.4 ± .26	1.72	4.87
Ulna	40	36.0	42.0	38.5 ± .29	1.86	4.83
Carpometacarpus	41	18.7	22.0	20.0 ± .13	.85	4.26
Phalanx 1, dig. II	41	9.1	11.1	9.9 ± .08	.53	5.33
Phalanx 2, dig. II	30	6.4	8.2	7.1 ± .08	.43	6.04
Furcula	17	30.6	35.9	32.8 ± .35	1.43	4.34
Coracoid	42	29.9	35.1	32.2 ± .22	1.42	4.42
Scapula	36	40.3	49.4	44.2 ± .37	2.24	5.08
Length of sternum	20	32.2	40.0	35.6 ± .54	2.42	6.79
Depth of carina	20	5.9	8.1	6.9 ± .14	.62	8.82

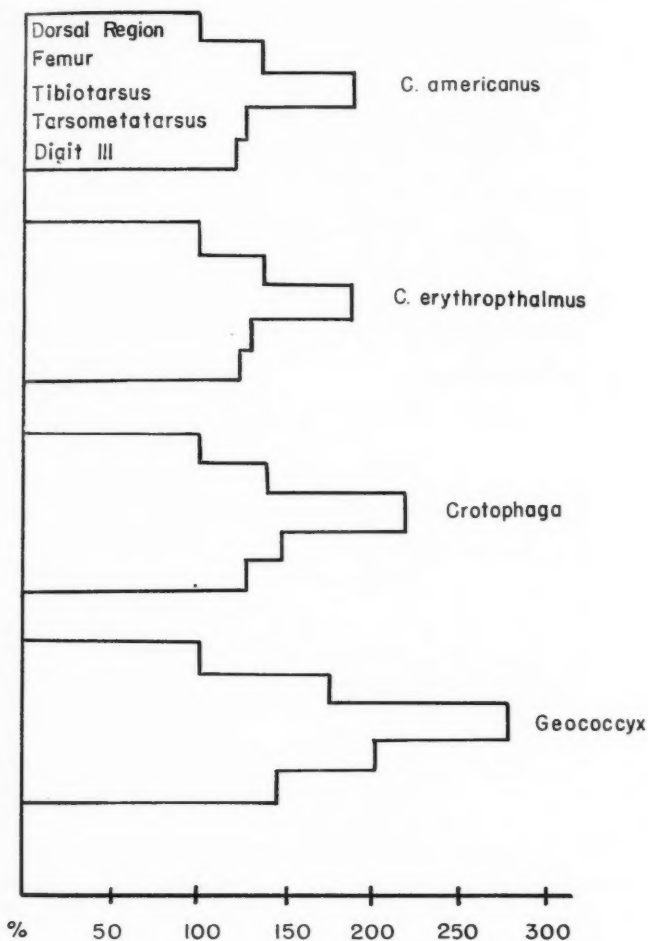


CHART I—Histograms illustrating proportions of the leg. Dorsal region/limb proportions based on length of dorsal region = 100%.

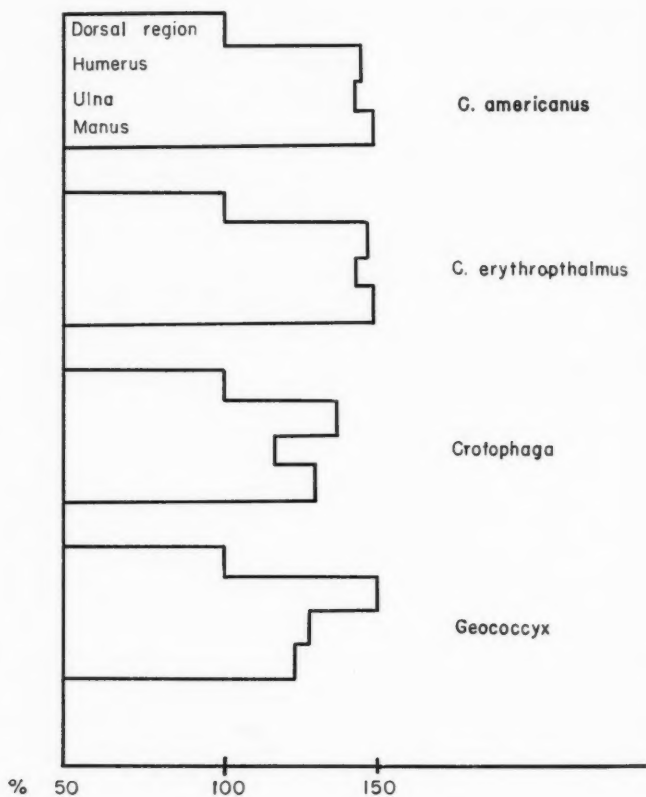


CHART II—Histograms illustrating proportions of the wing. Dorsal region/limb proportions based on length of dorsal region = 100%.

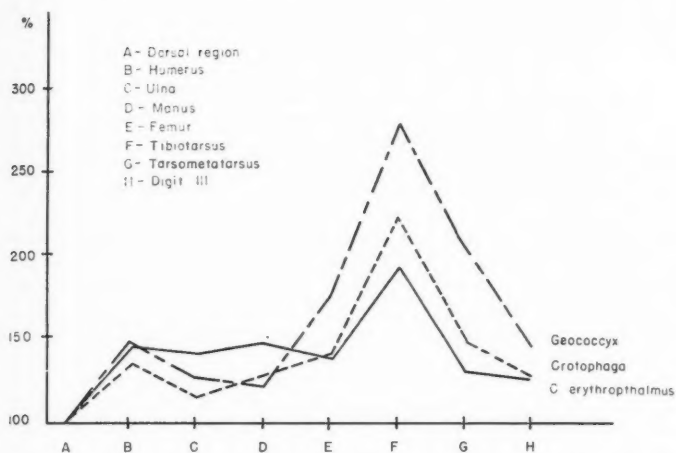


CHART III—Bildlichen Indices of dorsal region/limb proportions based on length of dorsal region = 100%.

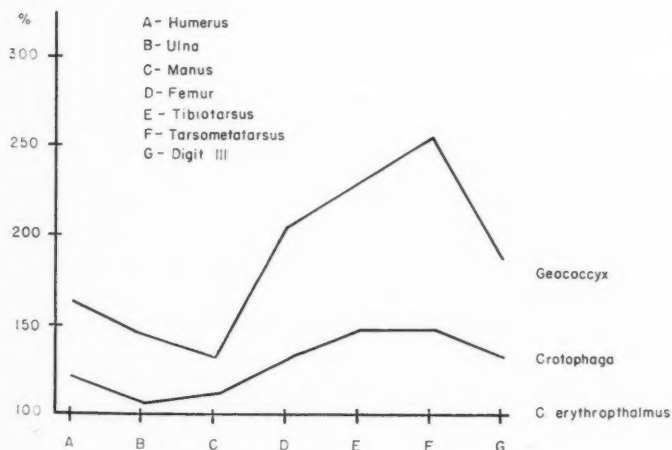


CHART IV—Bildlichen Indices of limb proportions based on the length of the several limb segments of *C. erythroptalmus* as standard.

Myology

INTRODUCTION

The terminology for the muscles used in this paper follows Hudson (1937), except that I have followed Wilcox (1948) in latinizing all terms and in modernizing spelling; and in keeping with modern trends hyphens have been omitted wherever practicable. *M. tibialis anterior* of Hudson, therefore, becomes *M. tibialis anticus*, and *anticus* and *posticus* replace *anterior* and *posterior* respectively; *M. peroneus* is shortened to *peroneus*. Hudson's paper was used as the basis for the nomenclature of muscles because of the thoroughness and clarity of his work. The need for uniformity in anatomical terminology is self-evident. For synonymy in muscle terminology the reader is referred to the papers of Hudson (1937) and Wilcox (1948). In the description of the myology of *Geococcyx* I have included also the names used by Shufeldt (1886b).

I have not dealt with the homology or innervation of the muscles. Hudson gave the homology of the muscles as presented by Gadow. The determination of homologies is a difficult task which in avian myology has not yet been accomplished. To add to this paper the homologies derived from earlier works appears superfluous. Little work has been done on the innervation of the pelvic musculature of birds and none has been done on that subject in the Cuculidae. To include such data on innervation as are available for other avian groups would be inexact and their inclusion here would be meaningless. The actions of pelvic muscles are given by Hudson (1937), Stolpe (1932) and others. I have discussed muscles and muscle groups which differ among the three genera and which are related to differences in locomotion.

No individual variation was found in the muscles of the legs of twelve specimens of *Coccyzus erythrophthalmus*. It is assumed, therefore, that four specimens each of *Crotophaga sulcirostris* and *Geococcyx californianus* would yield reliable information for the description of their muscles. Both legs of each specimen were dissected. I did not find any measurable differences between *C. erythrophthalmus* and *C. americanus*.

Since the musculature of the pelvic appendage of *Crotophaga sulcirostris* has not been described previously I have described its muscles more extensively than those of the other two genera. Therefore, in the several descriptions of muscles its muscles are described first, though structurally and in habits it logically falls between *Coccyzus* and *Geococcyx*.

DESCRIPTION OF PELVIC MUSCLES

MUSCULUS ILIOTROCHANTERICUS POSTICUS

This is a relatively large, stout, fusiform muscle located deep on the lateral surface of the anterior half of the ilium. It is hidden beneath the heads of the sartorius and iliobtibialis muscles. It is in the form of an oval fleshy mass which terminates caudally in a stout, tapering, truncated tendon.

In *Crotophaga sulcirostris* (Plates XV, XXII) the iliotorchantericus posticus muscle originates on the lateral aspect of somewhat more than the anterior half of the ilium over a narrow elliptical area which terminates anteriorly in a down-curved point on the anterior iliac process and posteriorly at the anterior iliac crest dorsal to the acetabulum.

The dorsal border of the area closely parallels the median dorsal ridge, and its ventral border forms a long convex curve well removed from both the ventral border of the ilium and the dorsal margin of the acetabulum. The fibers of this muscle run caudad horizontally, sloping only slightly ventrad and converging but little to a tendon which tapers from a maximum width of 3.5 mm. to a minimum width of 2 mm. and which inserts on a vertical ellipse on the lateral surface of the femur slightly distal to the trochanter.

In *Coccyzus erythrophthalmus* (Plates III, X) the ilioprochantericus posticus originates on the lateral aspect of the anterior half of the ilium over a broad cornucopiate area whose anterior point is on the anterior iliac process, whose ventral border parallels the ventral border of the ilium, whose rounded posterior end reaches the caudal part of the anterior iliac crest, and whose dorsal curvature reaches the median dorsal ridge. Its fibers slope caudoventrad and converge on a short tapered tendon about 1 mm. wide at its insertion which is on a vertical ellipse on the lateral surface of the femur directly opposite its head.

In *Geococcyx californianus* (Plate XXVI) the ilioprochantericus posticus (gluteus medius—Shufeldt, 1886b: 475) originates on the lateral aspect of the anterior three-fifths of the ilium over an elliptical area whose anterior portion is a slender triangular extension from this ellipse. The elliptical area is centered dorsal to the acetabulum, and the anterior triangular area is curved sharply downward at the anterior iliac process. The ventral border of the muscle roughly parallels the ventral border of the ilium at some distance away while its dorsal border follows the median dorsal ridge and is notched over its anterior extension in accordance with the ilium. The fibers of this muscle run caudolaterad in its anterior portion and laterad in its major mass converging in a short, strong tendon about 3 mm. in width which inserts on an elliptical elevation on the femur directly opposite its head.

The center of origin of this muscle in *Coccyzus* is near the center of the preacetabular portion of the ilium and none of its fibers originate dorsal to the acetabulum; therefore, all of its fibers protract rather than abduct the femur. In *Crotophaga*, though the center of origin of this muscle is well anterior to the acetabulum, a considerable portion of its fibers originate dorsal to the acetabulum and can serve only to abduct the femur. In *Geococcyx* the posterior area of origin of this muscle carries approximately half of its fibers and is centered dorsal to the acetabulum. In this species, therefore, the abductor action of the muscle would seem to have become fully as important as its protractor action.

MUSCULUS ILIOTROCHANTERICUS ANTICUS

This muscle, likewise hidden from view by the sartorius and iliotibialis, is a relatively small, caudoventrally directed, fleshy muscle on the lateral aspect of the ventral border of the preacetabular portion of the ilium. Its head is overhung laterally by the ventral border of the head of the ilioprochantericus posticus while its posterior half lies exposed ventral to that muscle.

In *Crotophaga sulcirostris* (Plates XV, XVI, XXII) the ilioprochantericus anticus muscle is conical in lateral view. Its fibers originate on a crescentic area which includes the posterior border of the anterior iliac process and half of the ventral portion of the lateral surface of the ilium anterior to the pectineal process. Its fibers converge from this relatively broad area of origin into a distinct tendon which tapers to a point of insertion on the lateral surface of the femur distal to that of the ilioprochantericus posticus and approximately opposite the ventral border of the acetabulum.

In *Coccyzus erythrophthalmus* (Plates III, IV, X) this muscle is a slender, fleshy strap whose fibers originate in a narrow line along the ventral border of the lateral surface of the ilium. The line begins anteriorly on the anterior iliac process and continues caudad about halfway to the pectineal process. Running caudoventrad, the muscle inserts by a short, broad tendon about 1 mm. wide on the lateral surface of the femur distal to the point of insertion of the ilioprochantericus posticus and approximately opposite the ventral border of the acetabulum.

In *Geococcyx californianus* (Plate XXVI) the ilioprochantericus anticus muscle (gluteus minimus—Shufeldt, 1886b: 475) has the same relative position, form and proportions as in *Crotophaga*.

In comparison between *Coccyzus* on the one hand, and *Crotophaga* and *Geococcyx* on the other, the iliotrochantericus anticus appears to be weaker but, because of its relatively longer belly, possessed of more range of contraction in the former species than in the latter two.

MUSCULUS ILIACUS

In *Crotophaga sulcirostris* (Plates XIX, XX, XXIII) the iliacus muscle is a short, slender strand of muscle fibers which originates at a point on the ventral border of the ilium slightly anterior to the acetabulum and runs ventrocaudolaterad. It passes anterior and mesial to the head of the femur, between the ambiens mesial to it and the femorotibialis medius lateral to it, to insert on the mesial surface of the femur opposite the ventral border of the pelvis. Its area of origin on the ilium is immediately caudal to that of the iliotrochantericus anticus and ventral to the center of that of the posticus. Its area of insertion on the mesial surface of the femur is about 3 mm. distal to the neck of the femur. The muscle is about 1 mm. wide, 7 mm. long, and entirely fleshy. It is the smallest muscle of the femoropelvic region.

In *Coccyzus erythrophthalmus* (Plates VII, VIII, XI) its relative size and position are similar to those in *Crotophaga*. In absolute size it is smaller, being approximately 0.75 to 1.5 mm. wide and 6 mm. long.

Though Shufeldt did not report this muscle in *Geococcyx californianus* (Plate XXVII), I found it to be similar in size and position to that in the other two genera. In *Geococcyx* it is about 2.5 mm. wide and 10 mm. long, and inserts by a distinct tendon on the caudomesial aspect of the femur about 4 mm. distal to the neck.

It may be noted that this muscle complements the iliotrochantericus anticus in contracting the femur but opposes it in rotatory effect, and that the two muscles are mostly fleshy in *Coccyzus* but each inserts by a tendon in *Geococcyx*.

MUSCULUS AMBIENS

The ambiens muscle is fundamentally similar in all three genera of cuckoos studied. It is a relatively long, thin, fleshy strap which arises on the pectineal process, runs distad along the femur mesial to the iliacus and the femorotibialis internus muscles, and becomes tendinous near the knee. Its tendon curves laterad over the anterior surface of the femorotibialis muscles, runs deep to the sartorius, passes through the patellar tendon and is reinforced by a slip from the biceps loop near the lateral surface of the head of the fibula.

In *Crotophaga sulcirostris* (Plates XVI, XVII, XIX) the ambiens arises from the pectineal process partly by an aponeurosis but largely by fleshy fibers. Its thin flat belly passes superficially down the anteromesial aspect of the thigh. A short distance above the condyles there forms on the anterior edge of its belly a thin tendon, covered mesially by the sartorius, which passes through the patellar tendon along the distal surface of the patella and crosses diagonally from the surface of the internal to that of the external condyle of the femur. From here it continues distad diagonally across the head of the fibula superficial to the third arm of the biceps loop, with which arm it is intimately fused. The ambiens tendon is further reinforced by one which arises from the posterolateral surface of the external condyle of the femur. This combined tendon serves for a part of the origin for *Mm. flexores perforati digiti II, III, and IV*.

In *Coccyzus erythrophthalmus* (Plates IV, V, VII) the ambiens arises from the pectineal process (spina pubica of Hudson) by a thin, short, narrow aponeurosis which gives way to a flat fusiform muscle. About three-fourths the way down the thigh the muscle converges onto a flat tendon which passes deep to the sartorius muscle, runs through the patellar tendon and crosses to the lateral aspect of the knee. From the knee the tendon passes caudadistad over the head of the fibula, a short distance below which it intimately fuses with the third arm of the biceps loop and is further reinforced by a tendinous band arising from the posterolateral surface of the external condyle of the femur. From this point of fusion, a flat tendon passes caudadistad to the posterior side of the fibula. It then passes mesial to the insertion of the biceps femoris muscle and continues about two-thirds of the way down the tibiotarsus, where it becomes inseparably

fused with the *Mm. flexores perforati digiti II, III, and IV*. This tendon serves as the sole origin for the *flexor perforatus digiti II*, the primary origin for the *flexor perforatus digiti IV*, and part of the origin for the *flexor perforatus digiti III*.

In *Geococcyx californianus* the ambiens muscle (ambiens—Shufeldt, 1886b: 477) has a relatively wide (5 mm.) and mostly fleshy origin from the lateral and ventral surfaces of the pectineal process. Its fleshy portion reaches a maximum width of 9 mm. and then tapers to a point on its tendon at a point about 33 mm. distal to the pectineal process. This tendon, concealed on the mesial aspect of the knee by the sartorius, appears on the anterior edge of its muscle about 10 mm. proximal to the termination of the fleshy portion. Passing through the deep surface of the patellar tendon along the mesial side of the patella, the tendon reaches the lateral aspect of the knee and runs diagonally across the neck of the fibula superficial to the attachment of the third arm of the biceps loop, with which arm it is intimately fused. About 8 mm. distal to the head of the fibula, the tendon joins the tendon of the *flexor perforans et perforatus digiti II* which arises from the posterolateral surface of the external condyle of the femur. As it passes distad the tendon broadens and serves as a part of the origin for *Mm. flexores perforati digiti II, III, and IV*.

The principal differences among these forms appears to be a replacement of the aponeurosis of origin by fleshy fibers and a recession of its fibrous portion proximad, a process that would appear to be a shift proximad of its center of gravity in correlation to facility of leg movement in running.

MUSCULUS SARTORIUS

The sartorius muscle is a comparatively large strap of muscle forming the extreme anterior border of the thigh, from the median dorsal ridge to knee.

In *Crotophaga sulcirostris* (Plates XIV, XIX, XXII) the sartorius muscle arises as a thin, broad sheet of fleshy fibers from the anterior portion of the median dorsal ridge and from adjacent tendons of the *M. longissimus dorsi* (Shufeldt, 1890: 278), but not from the spine of the last dorsal vertebra. The posterior half of the origin is by an aponeurosis which is intimately fused posteriorly with that of the iliotibialis muscle. Its insertion is by fleshy fibers on the anteromesial portion of the patellar tendon and on the head of the tibiotarsus above the inner cnemial crest.

In *Coccyzus erythrophthalmus* (Plates II, VII, X) the sartorius muscle arises mainly as a sheet of fibers from the median dorsal ridge. Its anterior border arises from the tendons of the *longissimus dorsi*, but none of it arises directly from the spine of the last dorsal vertebra. This origin is primarily fleshy. Its posterior border, however, arises by an aponeurosis which is intimately fused with the aponeurosis of the iliotibialis muscle. The proximal two-thirds of its belly is intimately connected with the anterior edge of the iliotibialis. It inserts primarily on the anteromesial side of the patellar tendon just distal to the patella, but its lateral border inserts on the head of the tibiotarsus by means of a small, thin, tendon above the inner cnemial crest. This tendon is intimately fused with the patellar tendon and may be considered a part of it.

In *Geococcyx californianus* (Plate XXVI) the sartorius muscle (sartorius—Shufeldt, 1886b: 472) arises semitendinous along about 15 mm. of the median dorsal ridge, from the superior aspect of the ilium dorsal to the anterior iliac process and from the posterior semitendinous portion of the *longissimus dorsi*. Contrary to Shufeldt, I found no part of it arising directly from the spine of the last dorsal vertebra. Its insertion is semitendinous on the patellar tendon and mostly fleshily on the head of the tibiotarsus directly above the inner cnemial crest. Some of its mesial fibers are intimately fused with the origin of pars interna of the gastrocnemius muscle.

This muscle is similar among the three genera as to origin, insertion, relationships and relative degree of development.

MUSCULUS ILIOTIBIALIS

This is a broad, thin muscle covering the greater portion of the lateral aspect of the thigh. It is the most superficial muscle in this region.

In *Crotophaga sulcirostris* (Plates XIV, XX, XXII) the iliotibialis muscle is a broad, flat sheet of flesh and aponeurosis covering the mid-lateral two-thirds of the entire length of the thigh. The muscle is fleshy along its posterior border and along all but a short portion at each end of its anterior border. Its two ends are strongly aponeurotic, a paddle-shaped aponeurosis forming its proximal portion, and a spatulate aponeurosis pointing proximad in the center of its distal two-thirds. Fleshy fibers separate these two aponeuroses. The aponeurosis of origin arises along a line running from the origin of the sartorius to that of the semitendinosus muscle. This line includes the anterior and posterior iliac crests and the median dorsal ridge. A portion of the aponeurosis also joins the distal half of the anterior iliac process, forming a stronger attachment than in *Coccyzus*. The anterior and posterior portions of the muscle continue fleshy to the distal end of the femur where they again become aponeurotic. The common tendinous band of the three portions contributes to the formation of the patellar tendon. Insertion of the patellar tendon is on a long narrow line on the proximal end of the rotular crest of the head of the tibiotarsus.

The origin and insertion of this muscle in *Coccyzus erythrophthalmus* (Plates II, VII, VIII, X) are similar to those in *Crotophaga*. In *Coccyzus*, however, the muscle differs in two respects from that in *Crotophaga*. In *Coccyzus* the muscle is thin and sheeplike throughout, the extreme posterior edge being slightly thicker. In *Crotophaga* there is an increase in the thickness of the leading edge of the belly as well as in the posterior third of the muscle. In *Coccyzus* the middle portion of the muscle is entirely aponeurotic, whereas in *Crotophaga* the aponeurotic portion is limited to the distal two-thirds of the central portion.

In *Geococcyx californianus* (Plate XXVI) the origin and insertion of the iliotibialis muscle (gluteus primus—Shufeldt, 1886b: 473) are similar to those in the other two genera. Differences existing in the form of this muscle between *Coccyzus* and *Crotophaga* are more pronounced in *Geococcyx*. In the latter species, the maximum thickness of the posterior half is about six times that of the anterior half and the thickness of the anterior edge of the muscle is about four times that in *Coccyzus*. In *Geococcyx* the aponeurosis of the muscle is limited to the distal half of its central portion.

The proportion of fleshy fibers to aponeurosis in this muscle, particularly in its central portion, progressively increases from *Coccyzus* through *Crotophaga* to *Geococcyx*. The border fibers are related to protraction and retraction of the thigh, and are strongly developed in all three genera, though the proportionately longer fleshy parts in *Crotophaga* and *Geococcyx* suggest a greater arc of thigh movement. Its central portion is related to balancing the axis on the head of the femur as a fulcrum. Entirely tendinous in *Coccyzus*, this portion appears to hold the knee at a fixed point with relation to the midsagittal plane. The progress of a fleshy segment in the other two forms suggests the presence of controlled movement of the knees with reference to this plane, a necessary movement for balance on one foot in the running gait. This development correlates to the progressive backward shift in the three genera of fleshy fibers in the iliotrochantericus posticus.

MUSCULUS FEMOROTIBIALIS EXTERNUS

This is a massive muscle covering the anterior and lateral surfaces of the femur. It is hidden from superficial view by the sartorius and iliotibialis muscles and is intimately fused with the mesially situated femorotibialis medius.

In *Crotophaga sulcirostris* (Plates XV, XIX, XX, XXII, XXIV, XXV) the femorotibialis externus arises mostly fleshy from the lateral aspect of the femur, beginning at a point distal to the area of insertion of the iliotrochantericus anticus and extending distad to a point a short distance beyond the region of proximal attachment of the biceps loop. Its belly is intimately fused anteromesially with that of the femorotibialis medius and its tendon contributes to the patellar tendon.

The patellar tendon encloses the patella, covers the knee joint and inserts on the rotular crest of the tibiotarsus. It is formed by the conjoined tendons of the iliotibialis, femorotibialis externus and femorotibialis medius muscles. The ambiens tendon passes diagonally through the deep surface of the patellar tendon.

In *Coccyzus erythrophthalmus* (Plates III, VII, VIII, X, XII, XIII) this muscle

arises on the lateral surface of the femur on an area which begins distal to the point of insertion of the ilirotrochantericus anticus and extends to the external condyle. It is completely fused along its anterior face with the femorotibialis medius muscle, and its tendon contributes to the patellar tendon. The primary insertion of the sartorius muscle is on the anteromesial side of the patellar tendon and a small aponeurosis of origin for the gastrocnemius pars interna also arises from it.

In *Geococcyx californianus* (Plates XXVI, XXVIII, XXIX) the femorotibialis externus muscle (vastus externus, extensor femoris—Shufeldt, 1886b: 475) arises as in the other two genera, mostly fleshy from the lateral aspect of the femur, beginning at a point immediately below that of the insertion of the ilirotrochantericus anticus and extending to the level of attachment of the proximal arm of the biceps loop. Three distinct semitendinous bands arise on the superficial surface of the distal half of its belly and insert on the lateral surface of the patellar tendon. The remainder of its belly continues as fleshy fibers to the external condyle, where its tendon arises and continues onward to contribute to the patellar tendon.

The patellar tendon is formed as in *Crotophaga* and inserts on the entire anterior surface of the head of the tibiotarsus including the inner cnemial crest, the rotular crest and the outer cnemial crest.

I was unable to detect any significant difference in form, structure or attachment of this muscle among the three genera.

MUSCULUS FEMOROTIBIALIS MEDIUS

This muscle appears to be an integral part of the femorotibialis externus. It lies on the anterior surface of the femur mesial to that muscle and is fused with it along the greater part of its mesial face.

In *Crotophaga sulcirostris* (Plates XV, XIX, XX, XXIII, XXIV) this muscle arises partly by tendinous fibers from the trochanteric ridge and by fleshy fibers from the entire anterior surface of the femur proximal to the level of attachment of the proximal arm of the biceps loop. Its fleshy portion inserts on the entire proximal surface of the patella and its tendon contributes to the patellar tendon. Laterally it is completely fused with the femorotibialis externus, but proximally the heads of the externus and internus are separated by the tail of the ilirotrochantericus anticus muscle.

In *Coccyzus erythrophthalmus* (Plates III, VII, VIII, XI, XII) the femorotibialis medius arises by an aponeurosis from the trochanter and the trochanteric ridge and by fleshy fibers from the distal three-fourths of the anterior face of the femur. Its fleshy portion inserts on the proximal end of the patella and its tendon contributes to the patellar tendon.

In *Geococcyx californianus* (Plates XXVI, XXVII, XXVIII) the femorotibialis medius muscle (cruracus, extensor femoris—Shufeldt, 1886b: 475) arises mostly semitendinous from the trochanteric ridge and fleshy from the anterior surface of the femur extending to the level of attachment of the proximal arm of the biceps loop. The fleshy portion inserts on the proximal end of the patella. The tendon contributes to the patellar tendon.

No significant differences in this muscle among the three genera were discovered.

MUSCULUS FEMOROTIBIALIS INTERNUS

This is a medium-sized fleshy muscle deep to the ambiens and against the posteromesial surface of the distal two-thirds of the femur.

In *Crotophaga sulcirostris* (Plates XIX, XXIII, XXIV, XXV) the femorotibialis internus muscle arises from the posteromesial aspect of the femur beginning along an area about 2 mm. proximal to the point of insertion of the iliacus and extending distal to the internal condyle. Its tendon arises on the posteromesial three-fourths of its belly and inserts on a tubercle on the anteromesial aspect of the head of the tibiotarsus mesial to the inner cnemial crest. The belly is bounded anteromedially by the femorotibialis medius and the ambiens, and posterolaterally by the pars interna of the adductor longus et brevis muscles. The tendon of insertion is covered mesially by the head of the gastro-

nemius pars interna and by the tail of the sartorius.

In *Coccyzus erythrophthalmus* (Plates VII, XI, XII, XIII) the femorotibialis internus arises fleshy from the posteromedial aspect of the femur, beginning at a point about 2 mm. distal to that of the insertion of the iliacus on the femur and extending distad to the mesial surface of the internal condyle. Its short, stout tendon inserts on a tubercle on the anteromedial aspect of the head of the tibiotarsus directly proximal to the point of origin of pars interna of the gastrocnemius muscle.

In *Geococcyx californianus* (Plates XXVII, XXVIII, XXIX) the femorotibialis internus (vastus internus—Shufeldt, 1886b: 478) arises fleshy from the posteromedial aspect of the femur over an area beginning a short distance (2 mm.) distal to the point of insertion of the iliacus and extending distad to the level of the mesial surface of the internal condyle. It inserts on a tubercle on the anteromedial side of the head of the tibiotarsus.

Hudson (1937: 21) discussed variations in the proximal extent of the area of origin of this muscle. I found that in *C. americanus*, *C. erythrophthalmus* and *Geococcyx* its area of origin begins about 2 mm. distal to the point of insertion of the iliacus, while in *Crotophaga* it begins about 2 mm. proximal to the point of insertion of the iliacus.

MUSCULUS PIRIFORMIS

The piriformis is a strong muscle which runs between the semitendinosus and the semimembranosus muscles and connects the proximal portion of the femur to the posterior end of the ilium and the pygostyle. It is a simple muscle in *Coccyzus*, but in *Crotophaga* and *Geococcyx* it consists of two parts: pars caudofemoralis and pars iliofemoralis, the former being a large horizontal muscle and the latter a smaller diagonal muscle.

In *Crotophaga sulcirostris* (Plates XIV, XV, XVI, XIX, XX, XXII, XXIII, XXV) this muscle consists of two structurally independent parts which will be discussed separately.

Pars caudofemoralis, a strong muscle which originates by a broad (5 mm.), flat tendon on the ventral surface of the pygostyle and the fascia covering the depressor muscles of the tail. This tendon is very short (about 4 mm.) and remains broad as it continues into the belly of the muscle. The belly runs cranioventrolaterad, passing between the semitendinosus and the semimembranosus and between the biceps femoris and the adductor longus muscles. Its insertion is mostly fleshy on the posterolateral aspect of the femur mesial to the area of insertion of its pars iliofemoralis described below.

Pars iliofemoralis, a muscle which arises by fleshy fibers along a relatively narrow line on the ventral and lateral surfaces of the posterior iliac crest posterior to the ilio-ischiatic fenestra (ischadic foramen of Hudson, 1937: 27). Its fibers pass cranioventrad superficial to the ischiofemoralis muscle to insert by fleshy fibers on the posterolateral aspect of the femur lateral to the insertion of pars caudofemoralis and about 1 mm. distal to the point of insertion of the ischiofemoralis tendon.

In *Coccyzus erythrophthalmus* (Plates II, III, IV, VII, VIII, X, XI, XIII) only *pars caudofemoralis* is present. It arises by a relatively narrow, short tendon in conjunction with the fascia of the depressor muscles from the ventrolateral aspect of the base of the disc of the pygostyle. This tendon, which is about 3 mm. long, becomes narrow and then gives way to a fleshy belly which passes cranioventrolaterad to the femur. The fleshy fibers insert on the posterolateral surface of the shaft of the femur distal to the point of insertion of the ischiofemoralis tendon.

In *Geococcyx californianus* (Plates XXVI, XXVII, XXIX) both parts of this muscle are present but are relatively poorly developed.

Pars caudofemoralis (femoro-caudal—Shufeldt, 1886b: 477) is a long, flat, spindle-shaped muscle about 45 mm. in length and 7 mm. in maximum width. It arises from the posterolateral aspect of the pygostyle by a flat semitendinous band which is intimately fused on its superficial surface with tough fascia extending from the pygostyle to the bases of the rectrices. It runs cranioventrolaterad to reach the femur, passing between the semitendinosus and the semimembranosus muscles. About 4 mm. from the femur it tapers

suddenly into a thin band of tendon about 2 mm. wide which appears to fuse with pars iliofemoralis of the same muscle. Shufeldt states that pars iliofemoralis joins pars caudofemoralis before their insertion. This tendon, however, can be teased away from the fleshy pars iliofemoralis and followed to its insertion mesial to but in contact with the insertion area of that muscle.

Pars iliofemoralis (accessory femoro-caudal—Shufeldt, 1886b: 477) arises fleshy from the ventromesial surface of the projecting posterior iliac crest and from a narrow, elliptical area on the dorsolateral surface of the ilium, beginning at the posterior border of the ilioischiatric foramen and extending caudad about 9 mm. The somewhat quadrangular belly passes sharply distad to insert mostly fleshy lateral to the pars caudofemoralis on the posterolateral aspect of the femur about 10 mm. distal to the trochanter.

Both pars caudofemoralis and pars iliofemoralis appear to retract the thigh, or, by corollary, to elevate the anterior portion of the axis, the head of the femur serving as a fulcrum. The far caudal point of origin of these muscles provides maximum leverage for such action in bilateral or synchronous movement of the legs. Their far caudal and mesial origins would, however, induce lateral movement of the axis in unilateral or alternate movement of the legs. The absence of pars iliofemoralis in *Coccyzus*, the appearance of pars iliofemoralis and the reduction in strength of pars caudofemoralis in *Crotophaga*, and the further strengthening of the former and reduction of the latter in *Geococcyx* provide interesting series of progression in vertical and regression in lateral pull on the axis which are correlated with the progression in unilateral and the regression in bilateral use of the legs among the three genera.

MUSCULUS SEMITENDINOSUS

This is a bulky muscle, triangular in cross section, on the posterolateral aspect of the thigh.

In *Crotophaga sulcirostris* (Plates XIV, XV, XVI, XIX, XX, XXII) the semitendinosus muscle arises mostly fleshy from the caudal portion of the lateral surface of the posterior iliac crest and from the transverse process of the first free caudal vertebra. The area of origin is bounded anteriorly by that of the iliotibialis. A little over half the distance down the thigh its belly is divided transversely by a caudodistally directed ligament into a proximal and a distal segment. The distal portion of the muscle, which lies anterior to this ligament, continues as the *accessorius semitendinosi* muscle to insert on the caudal and caudolateral aspect of the distal one-fourth of the femur, this area of insertion extending to that of the origin of pars externa of the gastrocnemius. The entire muscle lies mesial to the biceps loop and lateral to the area of insertion of pars externa of the adductor longus et brevis. The ligament which separates the two portions of the semitendinosus complex bends sharply downward behind the knee and a short distance below this region receives the insertion of the pars media of the gastrocnemius muscle. The main part of the separating ligament then continues distad to fuse with pars interna of the gastrocnemius. There is also a flat, thin, tendinous band (about 1 mm. wide) which arises from the proximal portion of this ligament and passes craniodistad over the mesial aspect of pars media of the gastrocnemius to insert on the caudomesial aspect of the tibiotarsus just below the internal articular surface.

In *Coccyzus erythrophthalmus* (Plates II, III, IV, VII, VIII, X) the semitendinosus arises by fleshy fibers from the posterior iliac crest and by fascia attached to the transverse processes of the first and second free caudal vertebrae. Hudson (1937: 22) called attention to the difficulty in determining the exact limits and relationships of this fascia. About two-thirds the way down the thigh the muscle is diagonally separated by a ligament into a proximal and a distal segment. The *accessorius semitendinosi* inserts on an area about 5 mm. long on the caudolateral aspect of the femur above the condyles. Behind the knee the separating ligament gives off a flat, tendinous branch slightly less than 1 mm. wide which continues craniodistad to insert on the caudomesial aspect of the tibiotarsus beneath the ligamental attachment (Howard, 1929: 323) which lies proximal to the insertion area of the semimembranosus. The distal part of the main ligament bends sharply downward to insert on pars interna and pars media of the gastrocnemius. There is no connec-

tion between this ligament and the tendon of insertion of the semimembranosus (Hudson, 1937: 23).

In *Geococcyx californianus* (Plate XXVI) the semitendinosus (semitendinosus—Shufeldt, 1886b: 476) arises mostly by fleshy fibers from the lateral and ventral surfaces of the posterior iliac crest and from the lateral surface of the ilium beneath this crest. It does not arise from the caudal vertebrae as in the other two genera. The ligament separating the proximal portion of the muscle from the accessorius semitendinosi or distal portion begins about one-third of the distance down the femur. The accessorius inserts on the posterior and posterolateral aspect of the distal half of the femur. The separating ligament gives rise to a 4 mm. wide, flat tendinous branch which continues in the straight course of the separating ligament, narrows to a width of about 2 mm. and inserts on the posteromesial aspect of the tibiotarsus about 3 mm. below the head. The main ligament bends sharply downward behind the knee and passes diagonally across the medial surface of the pars media of the gastrocnemius with which it is intimately fused. This ligament merges imperceptibly into the semitendinous continuation of pars media at the point where this head joins pars interna of the gastrocnemius. This distal continuation of the accessorius ligament, therefore, is less prominent than in either *Coccyzus* or *Crotophaga*. Shufeldt did not mention this portion of the ligament.

This muscle is the most powerful retractor of the thigh. It also flexes the knee by means of the fibular insertion of its ligament. In addition, the continuity of this ligament with pars media and pars interna of the gastrocnemius enables this muscle also to aid in extension of the tarsometatarsus. The progressive migration cranial in the three genera of the area of origin of this muscle and the consequently more nearly vertical action of its fibers reduces its tendency to produce lateral swing in the axis when the femur is retracted or the trunk elevated on the acetabular fulcrum.

MUSCULUS SEMIMEMBRANOSUS

The semimembranosus is a band-shaped muscle occupying the posteromesial aspect of the thigh. It is covered laterally by the semitendinosus and the accessorius semitendinosi muscles.

In *Crotophaga sulcirostris* (Plates XIV, XV, XVI XVII, XIX, XX, XXII, XXIII, XXV) this muscle arises laterally along a curved line on the posterior portion of the ischium about 2 mm. above the ischio-pubic fenestra. The anterior half of its head is aponeurotic and is covered laterally by the adductor longus et brevis pars externa; the posterior half is mostly fleshy. Its belly enters the musculature of the crus and gives way to a thin, flat tendon which passes between the pars interna and the pars media of the gastrocnemius to insert on an eminence on the mesial side of the tibiotarsus immediately distal to the inner cnemial crest. This muscle also gives off a semitendinous slip which inserts on the pars interna of the gastrocnemius at the point where the ligament of the accessorius semitendinosi joins that muscle.

In *Coccyzus erythrophthalmus* (Plates II, III, IV, V, VII, VIII, X, XI, XIII) the semimembranosus arises by an aponeurosis from the ventral border of the ischium posterior to the area of origin of the adductor longus et brevis pars externa and dorsal to that of the pars interna of that muscle. The course and relationships of the semimembranosus are the same as in *Crotophaga*. Insertion is by a flat, thin tendon on an eminence on the mesial side of the tibial shaft near the head. There is no accessory insertion of this tendon as in the other two genera.

In *Geococcyx californianus* (Plates XXVI, XXVII, XXIX) the semimembranosus (semimembranosus—Shufeldt, 1886b: 477) muscle arises mostly by fleshy fibers along a narrow curved line on the ventral surface of the ischium posterior to the origin of the adductor longus et brevis pars externa, and dorsal to the origin of the adductor longus et brevis pars interna. Distally, its belly enters the musculature of the crus and gives way to a very thin tendinous sheet which passes between pars media and pars interna of the gastrocnemius to insert along a curved line on the anteromesial aspect of the tibiotarsus about 7 mm. below the head. Just before the muscle enters the crus it gives off a semitendinous slip which inserts on pars media and pars interna of the gastrocnemius at their point of fusion. Shufeldt did not mention this accessory insertion.

No significant differences in the structure or relationships of this muscle were found among the three genera. The accessory insertion might be of taxonomic importance but can hardly be functionally significant.

MUSCULUS BICEPS FEMORIS

This is a heavy, triangular muscle located on the lateral aspect of the thigh under cover of the iliotibialis muscle.

In *Crotophaga sulcirostris* (Plates XV, XXII, XXV) this muscle arises from the posterior iliac crest, ventral to the area of origin of the posterior portion of the iliotibialis, and from the anterior iliac crest. The posterior two-thirds of its origin is fleshy, the anterior one-third is aponeurotic and overlies the posterior part of the origin of the iliotrochantericus posticus. This stout, triangular muscle lies along the posterolateral aspect of the thigh. Behind the knee it tapers into a strong tendon which passes through the biceps loop and inserts on a tubercle on the posterior surface of the fibula about 9 mm. distal to the head of that bone. The tendon lies superficial to the ambiens tendon and associated muscles and is covered laterally by the flexor perforans et perforatus digiti III.

The biceps loop is composed of two principal arms, a proximal arm which is attached to the lateral aspect of the femur about 3 mm. above the external condyle, and a distal arm which is attached laterally on the proximal end of the external condyle. The distal arm is intimately fused with the tendon of origin of pars externa of the gastrocnemius. A third smaller arm runs craniodistad from the bottom of the loop to become fused with the ambiens tendon and the tendinous origin of flexor perforatus digiti II and flexor perforatus digiti IV. By this compound tendon it then attaches to the head of the fibula (see description of *M. ambiens*).

In *Coccyzus erythrophthalmus* (Plates II, III, IV, X, XIII) this muscle arises mostly fleshily from the posterior iliac crest below the origin of the posterior third of the iliotibialis. Its anteriormost portion arises by a thin aponeurosis. The fibers of this muscle converge behind the knee into a strong, stout tendon which passes through the tendinous biceps loop. The biceps loop is formed as in *Crotophaga*. Insertion is on a tubercle on the posterior aspect of the fibula about 9 mm. below the head.

In *Geococcyx californianus* (Plates XXVI, XXIX) the biceps femoris (biceps flexor cruris—Shufeldt, 1886b: 476) arises deep to the iliotibialis as a semitendinous portion from the posterior region of the anterior iliac crest and the fascia of the iliotrochantericus posticus and as a fleshy portion partly from the lateral but mostly from the ventral surface of the posterior iliac crest. Behind the knee its fibers converge into a tendon which passes through the biceps loop and enters the musculature of the crus between the two heads of pars externa of the gastrocnemius. It inserts by a single tendon on a tubercle on the posterior face of the fibula. The biceps loop is formed as in the other two genera.

Hudson (1937: 25) mentioned that the origin of this muscle in *Coccyzus americanus* is limited to the "acetabular and post-acetabular ilium." This is true also for *C. erythrophthalmus*. In *Crotophaga*, however, its area of origin extends cranial on the anterior iliac crest for a distance of about 3 mm. In *Geococcyx* the cranial extension is even greater, running along the anterior iliac crest for a distance of about 10 mm. and also reaching the median dorsal ridge by means of an aponeurosis shared in common with the iliotrochantericus posticus.

This muscle is well developed in all three genera. Differences are limited to the extent of its origin and the degree of development of its belly. The point of insertion of its tendon with respect to the proximal end of the fibula is relatively the same in all three genera, although the power arm (see Richardson, 1942: 345) in *Coccyzus* may exhibit a slight advantage over that in *Crotophaga* and *Geococcyx*. The length of the biceps loop also is relatively the same in the three genera.

MUSCULUS ISCHIOFEMORALIS

This is a triangular muscle lying deep on the lateral surface of the ischium.

In *Crotophaga sulcirostris* (Plates XVII, XXII) it arises fleshy from almost the entire lateral surface of the ischium and from the posterior and ventral borders of the ilio-ischiatic fenestra. A tendon forms on the superficial surface of its belly and inserts

on a ridge on the lateral surface of the femur between the insertions of the iliotrochantericus posticus and anticus. The fibers arising from the posterior border of the ilio-ischiatic fenestra pass craniodistad to fuse with the main belly slightly beyond its midpoint. Fibers arising from the anteroventral edge of the ischium immediately caudal to the obturator foramen and deep to the belly and tendon course along the ventral surface of the tendon but remain fleshy to their point of insertion distal to that of the tendon.

In *Coccyzus erythrophthalmus* (Plates IV, VIII, X) the ischiofemoralis muscle arises by fleshy fibers from most of the dorsolateral surface of the ischium posterior to the obturator foramen and from the posteroventral surface of the posterior iliac crest. It inserts by a short, flat tendon on the posterolateral surface of the femur between the areas of insertion of the iliotrochantericus posticus and anticus, and proximal to the areas of origin of the femorotibialis externus and the insertion of pars caudofemoralis of the piriformis muscle.

In *Geococcyx californianus* (Plate XXVI) the ischiofemoralis (obturator externus—Shufeldt, 1886b: 477) arises fleshy from the lateral surface of the ischium on an area lying dorsal to the semimembranosus and the adductor longus et brevis pars externa and extending from the obturator foramen to the caudal end of the ischium. A broad, flat tendon forms on the superficial face of the muscle and inserts on the posterolateral aspect of the femur immediately distal to the point of insertion of the iliotrochantericus posticus.

This muscle shows the same relationships and relative development among the three genera.

MUSCULUS OBTURATOR INTERNUS

This flat, triangular muscle lies on the mesial surface of the ischium and pubis.

In *Crotophaga sulcirostris* (Plates XIX, XXII, XXIII, XXV) the obturator internus muscle arises mainly on the mesial surface of the ischium and pubis, though a few of its fibers are attached to the ischio-pubic membrane and a few come from the posteroventral border of the ilio-ischiatic fenestra. Its stout tendon passes through the obturator foramen and inserts on the posterolateral surface of the trochanter. Two distinct tendons and a third smaller one form on the midpoint of the deep surface of its belly and fuse after emerging from the obturator foramen.

In *Coccyzus erythrophthalmus* (Plates V, VII, X, XI, XIII) this muscle arises from the mesial surface of the ischium and pubis, the posteroventral border of the ilio-ischiatic fenestra and the ventral surface of the ilium dorsal to the posterior boundary of the ilio-ischiatic fenestra. Hudson (1937: 27 and 77) mentions this latter origin in *Fulica*, *Porzana carolina* and *Colinus* but does not mention it for *Coccyzus americanus*. In the latter species and in *C. erythrophthalmus*, I found that this muscle arises from the ventral surface of the dorsal portion of the ilium, but I was unable to determine whether any part of its origin was from the ischio-pubic membrane. In each case, three tendons are formed on the deep surface of the belly of the muscle. The three tendons fuse and pass through the obturator foramen accompanied by some fleshy fibers which surround the tendon. The single tendon inserts on the posterolateral side of the trochanter between the two points of insertion of the obturator externus.

In *Geococcyx californianus* (Plates XXVI, XXVII, XXIX) the obturator internus (obturator internus—Shufeldt, 1886b: 478) arises from the mesial surface of the ischium and pubis, from the posterodorsal border of the ilio-ischiatic fenestra and from the posteroventral wall of the renal depression. Also, a few of its fibers appear to arise from the ischio-pubic membrane. The dorsal portion of the muscle more than half fills the ilio-ischiatic fenestra. Three distinct tendons of unequal size are formed on the deep surface of the belly and pass through the obturator foramen. The largest of these tendons receives fibers from the pubis and the ventral portion of the ischium, the medium sized one receives fibers primarily from inside the pelvis, and the smallest tendon, lying between the other two, receives fibers from the posterior border of the ilio-ischiatic fenestra and the dorsal portion of the ilium. At the point of emergence from the obturator foramen, the smallest tendon unites with the largest, and a short distance beyond the medium-sized tendon unites with the main tendon. This stout, single tendon inserts in a depression on the posterior aspect of the femur immediately below the trochanter. Fleshy fibers arising

on the pubis pass through the obturator foramen with the main tendon and insert with it. Shufeldt did not mention the origin of any part of this muscle from the postero-ventral wall of the renal depression nor the presence of three tendons.

This muscle has similar features in all three genera, exhibiting no difference which might be of functional importance.

MUSCULUS OBTURATOR EXTERNUS

The obturator externus muscle is a very small muscle situated in the angle between the proximal end of the femur and the lateral surface of the ischium and pubis posterior to it. Arising on the border of the obturator foramen and passing directly to the femur, it is hidden underneath all other muscles in that region.

In *Crotophaga sulcirostris* (Plates XVIII, XXV) this short fleshy muscle originates on the ventral and anterior borders of the obturator foramen and passes laterad mesial to the tendon of the obturator internus to insert by a slight tendon on the femur distomesial to the tendon of the obturator internus. It is unbranched throughout, all of its fibers originating over a continuous area and all inserting by a single tendon.

In *Coccyzus erythrophthalmus* (Plates V, X, XIII) the obturator externus is bipartite in form. A larger part of it originates on the ventral border and a smaller part originates on the dorsal border of the obturator foramen. Although the fibers of origin are not clearly separate, two parts of unequal size are distinct throughout the remainder of the muscle. The larger tail is short, wide and fleshy and inserts mainly by a slip about 2 mm. wide onto the caudolateral aspect of the femur at a point mesial to that where the obturator internus inserts. Some of its more proximal fibers, however, insert directly on the tendon of the obturator internus. The smaller part is a fleshy, triangular mass of fibers which runs dorsomesial to the tendon of the obturator internus and inserts by a semitendinous attachment on the trochanter proximal to but in contact with that tendon.

In *Geococcyx californianus* (Plate XXIX) the obturator externus (gemellus—Shufeldt, 1886b: 478) is entirely fleshy and about 6 mm. long. It originates on the ventral border of the obturator foramen and inserts on the femur at a point about 1 mm. distal to that for the insertion of the obturator internus. Contrary to Shufeldt's description, I did not find any part of this muscle inserting with the tendon of either the obturator internus or the ischiofemoralis.

The obturator externus in *Coccyzus* is in reality two muscles, both with somewhat tendinous insertions. In *Crotophaga* and *Geococcyx*, however, only the ventral portion or muscle persists with a tendinous insertion in the former but a fleshy one in the latter. It is essentially antagonistic to the ilirotrochantericus anticus but shows a tendency towards loss of a tendon of insertion, suggesting a greater range of rotation of the femur in *Crotophaga* and *Geococcyx* than in *Coccyzus*.

MUSCULUS ADDUCTOR LONGUS ET BREVIS

This is the most mesial of the thigh muscles located posterior to the femur. It consists of two distinct parts which are not fused at any point although they are in close contact throughout most of their extent.

In *Crotophaga sulcirostris* (Plates XVI, XVII, XX, XXII, XXV) pars externa of the adductor longus et brevis arises mostly by fleshy fibers from the lateral surface of the ventral edge of the ischium. Its area of origin lies anterior to that of the semimembranosus and dorsal to that of pars interna of the adductor longus et brevis and extends cranial to the obturator foramen. It inserts by fleshy fibers on the posterior surface of the distal two-thirds of the femur, on an area which extends from the point of insertion of the piriformis to within 6 mm. of the distal end of the femur. It is bounded laterally by the piriformis, semitendinosus and accessorius semitendinosi, and mesially by pars interna of the adductor longus et brevis.

Pars interna (Plates XVII, XVIII, XIX, XXII, XXV) arises primarily by an aponeurosis from the ventral border of the anterior two-thirds of the ischium which includes the dorsal border of the ischio-pubic fenestra and an area which extends cranial to the obturator foramen. The fibers of the anterior fifth of its origin are fleshy. Pars externa and the semimembranosus muscles arise dorsal to pars interna. It inserts in part

semitendinous on the posterior aspect of the distal two-thirds of the femur, but mostly by fleshy fibers on the posteromesial ridge of the internal condyle distal to the point of origin of pars media of the gastrocnemius.

In *Coccyzus erythrophthalmus* (Plates IV, V, VIII, X, XI, XIII) pars externa arises mostly by fleshy fibers along a narrow line beginning at the obturator foramen and running caudad about 3 mm. along the ventral border of the ischium above the ischio-pubic fenestra (foramen oblongum of Hudson, 1937: 28). Posteriorly its head is intimately fused with that of the semimembranosus. Its insertion is fleshy on the distal two-thirds of the posterior surface of the shaft of the femur, distal to the point of insertion of pars caudofemoralis of the piriformis. The area of its insertion is bounded laterally by that of the femorotibialis externus and mesially by that of the femorotibialis interna and of pars interna of the adductor longus et brevis.

Pars interna (Plates V, VI, VII, X, XI, XIII) arises primarily by an aponeurosis from a narrow line ventral to the origin of pars externa and the semimembranosus. This line extends along the ventral border of the ischium from the obturator foramen to a point slightly farther caudad than the origin of pars externa. The anterior third of the muscle soon becomes fleshy, but its posterior two-thirds remain aponeurotic for about a third of the distance down the thigh. It inserts on the distal half of the caudomesial surface of the femoral shaft mesial to the pars externa, and on the proximal end of the internal condyle of the femur. The proximal half of this insertion is semitendinous and the distal half is fleshy.

In *Geococcyx californianus* (Plates XXVI, XXVII, XXIX) pars externa (adductor longus—Shufeldt, 1886b: 478) arises mostly by fleshy fibers from the ventral border of the ilium along a line extending from the obturator foramen to the area of origin of the semimembranosus. It inserts by fleshy fibers on the posterolateral aspect of the femur on an area which lies lateral to that of the pars interna. This area begins about 1 mm. below the point of insertion of the piriformis and extends distad about 25 mm.

Pars interna (adductor magnus—Shufeldt) (Plates XXVI, XXVII, XXIX) arises primarily by an aponeurosis from the ventral edge of the ischium, along the dorsal border of the ischio-pubic fenestra. The anterior fifth of its origin is partly fleshy. Its insertion is semitendinous on the posteromesial aspect of the distal two-thirds of the femur and on the posteromesial ridge of the internal condyle adjacent to the point of origin of pars media of the gastrocnemius.

No significant differences were found among the three genera in the form of the two parts of this muscle.

MUSCULUS TIBIALIS ANTICUS

This is the most powerful muscle on the anterior aspect of the crus. In *Coccyzus* it is also the most superficial muscle in this region, whereas in *Crotophaga* and *Geococcyx* it is covered by the peroneus longus.

In *Crotophaga sulcirostris* (Plates XIV, XV, XVI, XIX, XX, XXII, XXIII, XXIV) the tibialis anticus muscle arises by two distinct heads, a larger tibial and a smaller femoral head. The tibial head arises mostly by fleshy fibers from the inner cnemial crest, the rotular crest, the outer cnemial crest, from the fascia covering the knee, and from a long narrow line on the anteromesial aspect of the tibiotarsus. The long, spindle-shaped femoral head arises from the distal apex of the external condyle of the femur by a strong tendon which passes distad deep to the ambiens tendon and between the outer cnemial crest and the head of the fibula, about 2 mm. below which point this head becomes fleshy. The two heads fuse around a flat tendinous band about halfway down the crus. This tendon runs down the deep surface of the muscle on the anterior surface of the tibiotarsus. Just above the condyles it passes under a strong fibrous loop, the ligamentum transversum (Stolpe, 1932: 213 and Richardson, 1942: 346), in company with but superficial to the tendon of the extensor digitorum longus. The tendon inserts as a single stout tendon on a tubercle on the anteromesial aspect of the tarsometatarsus about 4 mm. distal to the proximal articular surface of that bone.

In *Coccyzus erythrophthalmus* (Plates II, III, IV, VII, VIII, X, XII) the femoral head of this muscle arises on the distal apex of the lateral condyle of the femur by a flat

tendon. The tibial head arises by fleshy fibers from the rotular crest below the insertion of the patellar tendon and on the anterior surface of the inner cnemial crest. These two heads fuse into a fleshy belly about 11 mm. distal to the rotular crest. Shortly above the condyles this belly narrows abruptly into a strong tendon which passes beneath the ligamentum transversum. The tendon inserts on a tubercle on the anteromesial aspect of the tarsometatarsus about 4 mm. distal to the proximal articular surface of that bone. Contrary to Hudson's statement for *C. americanus* (1937: 30 and 72), I was unable to demonstrate an accessory tendon of insertion in either *C. americanus* or *C. erythrophthalmus*.

In *Geococcyx californianus* (Plates XXVI, XXVIII) most of the tibial head of the tibialis anticus (tibialis anticus—Shufeldt, 1886b: 479) arises by fleshy fibers from a narrow line on the inner cnemial crest, from the rotular crest, and from the anterior surface of the outer cnemial crest. Its fibers attach to the semitendinous sheets and bands arising from these same areas, attachments which are shared with the peroneus longus muscle. As in the other two genera, the femoral head arises by a strong, flat tendon from a pit at the apex of the external condyle. This tendon passes distad between the outer cnemial crest and the head of the fibula and quickly changes into a wide, thin tendinous band which runs down the deep surface of the belly of the muscle. The two heads fuse about 30 mm. below the head of the tibiotarsus. The very stout tendon passes under the ligamentum transversum just above the condyles and inserts on a tubercle on the anterior surface of the tarsometatarsus about 4 mm. below the proximal articular surface of that bone.

The tibialis anticus is equally well developed in the three genera. It is the sole flexor of the tarsometatarsus. Differences in the relative point of insertion may be functionally important. In each species, the tendon inserts about 4 mm. distal to the proximal articular surface of the tarsometatarsus. When we consider that the length of this bone in *Crotophaga* is about 50 per cent and in *Geococcyx* is about 150 per cent greater than in *Coccyzus* it becomes evident that in *Coccyzus* the tibialis anticus can exert a much greater force on the tarsometatarsus than it can in either of the other two forms. This situation stands in sharp contrast to that found by Richardson (1942: 345-346) in tree-trunk foraging birds. He found not only a range of variation in the point of insertion of the tendon of this muscle but also a modification in the length of the loop of the ligamentum transversum. In the Cuculidae, the slight difference in the length of this loop can be attributed only to the difference in size in these three birds.

MUSCULUS EXTENSOR DIGITORUM LONGUS

This is the deepest muscle on the anterior surface of the tibiotarsus and lies directly underneath the tibialis anticus.

In *Crotophaga sulcirostris* (Plates XVII, XIX, XX, XXII, XXIII, XXIV) this muscle has a short, triangular, fleshy body deep against the anterior face of the proximal third of the tibiotarsus. From it arises a long slender tendon which runs down the anterior surface of the leg for the remaining length of the tibiotarsus and the full length of the tarsometatarsus. At the distal end of the tarsometatarsus the tendon expands into a triangular sheet from the three corners of which a digital dorsal tendon passes down digits II, III and IV.

The muscle arises by fleshy fibers from the inner cnemial crest, the rotular crest, and along about 20 mm. of the anterior surface of the tibiotarsus. About a third the way down the tibiotarsus it gives over to a tendon. Following close along the anterior surface of the tibiotarsus, near the distal end of that bone the tendon passes beneath and is held in place by the ligamentum transversum, deep to the tibialis anticus tendon, then under a bridge of bone and between the condyles to the anterior aspect of the tarsometatarsus. On the tarsometatarsus, the tendon immediately enters a ligament-covered, short bony groove and emerges from it in position mesial to the tibialis anticus tendon and superficial to the short extensor muscles along the tarsometatarsus.

At the level of the base of digit I the tendon, now about 1 mm. in width, expands into a triangular sheet with sides about 3 mm. long. The main tendon forms the apex of the triangle, the dorsal tendon of digit II arises also at its apex, that to digit III arises at the inner end of its base, and that to digit IV arises at the outer end of its base.

Above the joint between the two most proximal phalanges of digit II, its tendon forks into a pair of lateral branches which reunite at their insertion on the proximal end of the terminal or ungual phalanx. Near its base the inside (mesial) branch of digital tendon II sends a slip to insert on the proximal end of the subterminal phalanx.

The dorsal tendon to digit III is split into two strands completely to its base. The branches follow their respective sides of the dorsal aspect of digit III to the proximal end of its terminal phalanx, where they unite and insert in common. At each of the other two nearest terminal joints of the digit the inner branch expands and gives off a slip which is joined by a slip from the outer branch, and inserts on the inner surface of the joint.

The outer basal corner of the tendon triangle extends laterad as far as the center of the most proximal phalanx of digit IV, where it forks into two only partially distinct lateral digital branches which terminate together in a common insertion on the proximal end of the terminal or ungual phalanx. Each of these branches gives off three slips, one to the proximal end of each of the other three nearest terminal phalanges of digit IV. The two branches of this tendon are interconnected by a web of fibers, and form an imperfect hemisheath on the dorsal surface of the digit. Likewise, its slips are obscure and form diffuse insertion sheaths around the four interphalangeal joints.

On each digit an automatic ungual extensor ligament arises on the dorsal surface of each subterminal phalanx and inserts in common with the fused branches of the dorsal digital tendon on the proximal end of the ungual phalanx.

In *Coccyzus erythrophthalmus* (Plates V, VII, VIII, X, XI, XII) the extensor digitorum longus muscle and tendons occupy the same relative position as in *Crotophaga sulcirostris*. Its fleshy portion is relatively longer and slenderer, however, occupying and arising from about the proximal half of the tibiotarsus. The triangular area of its tendon is relatively more pronounced, increasing from a tendon width of 0.4 mm. to a maximum width of 3 mm., and its apex is much higher and more acute. In addition, the base of the triangle is imperfectly split by two thinly webbed areas between the base of the tendon to digit IV and those of the tendons to the other two digits. Between these two near-foramina and on the margin of the distal one are two strong, fibrous bands connecting the base of the tendon of digit IV to that of digit III.

The tendon to digit II arises on the inner side of the triangle and without splitting runs to its terminal insertion on the ungual phalanx, giving off a single slip to the sub-terminal joint in passing.

The tendon to digit III in *Coccyzus* differs most widely from that in *Crotophaga*. It has three parallel branches of unequal strength. The strongest is in median position on the digit and runs to the proximal end of the terminal phalanx and inserts there in common with the second in strength, which runs along the inner surface of the digit. The weakest runs along the outer surface of only the proximal phalanx. The median branch sends a slip to the interphalangeal joints second and third from the digit tip. The outer branch arises from the common base of the other two branches and from the base of digit tendon IV by a forked tendinous root whose limbs bound the distal thin area on the triangle. It terminates at the proximal interphalangeal joint in two slips, one to the base of the slip to that joint from the median branch and one to insert in common with it.

The tendon to digit IV splits and its two branches insert terminally as in *Crotophaga*. Each branch, however, gives only two slips to the more proximal interphalangeal joints, the outer branch supplying the more proximal two and the inner branch the more distal two of these—thus, only the third joint from the tip of the digit receives slips from both branches.

As in *Crotophaga*, an automatic ungual extensor ligament arises on each subterminal phalanx of digits II, III, and IV and inserts in common with the dorsal digital tendon on its distal phalanx.

In *Geococcyx californianus* (Plates XXVI, XXVII, XXVIII) the extensor digitorum longus muscle (extensor longus digitorum—Shufeldt, 1886b: 480) closely resembles that of *Crotophaga* in form and area of origin, though in *Geococcyx* its more mesial fibers originate on a dense sheet of tendinous tissue which arises on the ventral surface of the inner cnemial crest and inserts on a narrow line along the anteromesial border of the tibiotarsus, and which is intimately related to the peroneus longus and the tibialis anticus

muscles. Its tendon bears the same relations to the surrounding parts as does that in both *Coccyzus* and *Crotophaga*. About 12 mm. above the distal end of the tarsometatarsus, the tendon bifurcates, the two branches being interconnected by connective tissue. The internal branch supplies digit II and gives another branch to digit III, and the external branch supplies digits III and IV. The dorsal digital tendons are similar to those in *Crotophaga* except that only a single tendon passes down the dorsal surface of digit IV.

An automatic ungual extensor ligament arises on the dorsal surface of the subterminal phalanges of digits II and III and inserts with the extensor tendon on the proximal end of the ungual phalanges of those digits. In addition, an automatic extensor ligament arises from the midportion of the dorsal surface of each phalanx of digit IV and inserts on the dorsal surface, proximal end of the phalanx next anterior to it.

In this muscle, diameter appears progressively to yield to length, suggesting increase in extension and spread of the toes, an adaptation to standing on a flat surface rather than perching on a limb. Minor variations in digital tendons are not considered to be functionally important.

MUSCULUS PERONEUS LONGUS

In *Crotophaga sulcirostris* (Plates XIV, XV, XIX, XXII, XXIII, XXIV) this muscle arises by a flat tendinous band from the outer surface of the outer cnemial crest, by an aponeurosis from the rotular crest, the inner cnemial crest, the fascia covering the knee, from a long narrow line along the anteromesial aspect of the tibiotarsus for a distance of about 25 mm. (in common with tibialis anticus), and from the lateral surface of the spine of the fibula; semitendinous from a long narrow line on the lateral surface of the tibiotarsus; and fleshy from the distal end of the tibiotarsus. It is intimately fused with the peroneus brevis and the flexor digitorum longus muscles. Some of the fleshy fibers accompany the tendon to the proximal end of the condyles. Shortly beyond this point the tendon bifurcates into a short branch, which inserts on the distolateral corner of the tibial cartilage, and a longer branch which continues distad over the external condyle superficial to the tendon of the peroneus brevis. About 6 mm. below the head of the tarsometatarsus, the longer branch joins the tendon of the flexor perforatus digiti III.

The peroneus longus is much better developed in *Crotophaga* than in *Coccyzus*, completely enveloping the deeper muscles on the proximal half of the anterolateral and anterior aspects of the crus.

In *Coccyzus erythrophthalmus* (Plates II, III, X, XII) the peroneus longus muscle arises tendinous by a thin band from a small area on the lateral surface of the outer cnemial crest and fleshy from the lateral surface of the spine of the fibula and a small area on the lateral surface of the distal third of the tibiotarsus. It is intimately fused with the peroneus brevis and the flexor digitorum longus muscles. Its main tendon bifurcates just above the condyles. The shorter branch expands and inserts on the tibial cartilage. The longer branch passes distad, over the external condyle and the tendon of the peroneus brevis, to the posterior side of the tarsometatarsus where it joins the tendon of flexor perforatus digiti III about one-fourth the distance down the bone.

In *Geococcyx californianus* (Plates XXVI, XXVII, XXVIII) the peroneus longus muscle (peroneus longus—Shufeldt, 1886b: 474) arises semitendinous from the inner cnemial crest, the rotular crest, the outer cnemial crest and along a narrow line on the anteromesial aspect of the tibiotarsus by a semitendinous sheet shared with the tibialis anticus and extensor digitorum longus muscles. It also arises by a tendinous band from the lateral surface of the spine of the fibula and a long, narrow line on the lateral surface of the tibiotarsus. It is intimately fused on its deep surface with the tibialis anticus, peroneus brevis and the flexor digitorum longus muscles. Tendinous fibers pass from the posterior side of the distal half of the main tendon to insert on the proximal half of the lateral surface of the tibial cartilage. The long tendon fuses with the tendon of the flexor perforatus digiti III about 9 mm. below the head of the tarsometatarsus. This muscle is even more strongly developed in *Geococcyx* than in *Crotophaga* and completely envelops the deeper muscles on the anterior and anterolateral aspects of the crus.

The peroneus longus muscle aids in extension of the tarsometatarsus and, because of

its connection with the tendon of the flexor perforatus digiti III, in flexion of digit III.

MUSCULUS PERONEUS BREVIS

This muscle lies along the posterolateral border of the tibialis anticus and deep to the peroneus longus muscle.

In *Crotophaga sulcirostris* (Plates XIV, XV, XVI, XXII, XXIV) the peroneus brevis muscle is a slender strand which arises semitendinous from the anterior surface of the spine of the fibula and fleshy from the anterolateral aspect of the tibiotarsus along a narrow line which extends to within about 10 mm. of the distal end of that bone. It is intimately fused with the peroneus longus. Immediately above the external condyle its tendon passes beneath a fibrous band, after which it continues diagonally over the lateral surface of the external condyle deep to the long tendon of the peroneus longus muscle, to insert on a tubercle on the posterolateral aspect of the head of the tarsometatarsus.

In *Coccyzus erythrophthalmus* (Plates II, III, IV, X, XII) the peroneus brevis is a fusiform muscle which arises from the anterior surface of the spine of the fibula and from the lateral surface of the tibiotarsus from the point of insertion of the biceps femoris tendon to a point about three-fourths the way down the bone. Its posterior border parallels and arises from the spine of the fibula. Its belly gives way to a stout tendon which has the same relationships and insertion as in *Crotophaga*.

In *Geococcyx californianus* (Plates XXVI, XXVIII) the peroneus brevis (tibialis posticus—Shufeldt, 1886b: 481) is a long, thin muscle which arises semitendinous from the anterior surface of the spine of the fibula and from a narrow area on the anterolateral surface of the tibiotarsus to within 18 mm. of the distal end of that bone. It also arises fleshy from the adjacent area on the tibiotarsus. Its semitendinous origin is shared with the distal portions of the peroneus longus and the flexor digitorum longus muscles. Its tendon passes under a heavy, fibrous sheath on the anterolateral surface of the tibiotarsus immediately above the external condyle and thence across the lateral surface of the condyle under the long tendon of the peroneus longus to insert on a tubercle on the posterolateral corner of the head of the tarsometatarsus.

MUSCULUS GASTROCNEMIUS

This is the largest and most superficial of the muscles on the posterior aspect of the crus. This muscle complex is composed of three major parts.

In *Crotophaga sulcirostris* (Plates XIV, XIX, XX, XXII, XXIII, XXV) the gastrocnemius muscle forms a crescent which covers the other posterior muscles of the crus. It is composed of three parts, one with two heads and each of the others with one, all of which unite in a single tendon (Tendo Achillis).

Pars externa, the lateral division of the gastrocnemius, arises by two heads. Its lateral head originates on a strong tendon which is attached to a tubercle on the proximal end of the external condyle of the femur and is intimately fused mesially with the distal arm of the biceps loop. Its smaller, mesial head arises by a flat tendon from the intercondyloid region of the femur and passes distad mesial to the biceps loop and tendon. The two heads fuse at about the level of insertion of the biceps tendon, which is about 10 mm. below the head of the tibiotarsus.

Pars media of the gastrocnemius is a short bundle of fleshy fibers which arises from the posterior surface of the internal condyle of the femur. It is intimately fused with the distal end of the adductor longus et brevis pars interna and the accessorius semitendinosus muscles, and its belly cannot with certainty be separated from that of the accessorius. It inserts on the ligament which separates the accessorius from the semitendinosus muscle. The tendon of the semimembranosus passes between the pars media and the pars interna.

Pars interna of the gastrocnemius has a massive head which arises fleshy from the mesial surface of the inner cnemial crest and partly semitendinous from the mesial side of the patellar tendon distal to the patella. Beginning at the level of the area of insertion of the semimembranosus muscle, pars interna and pars externa are joined by a common fascia, and three-fourths the way down the crus their fibers converge into a common tendon which passes over the posterior surface of the tibial cartilage to insert on the posterior surface of the hypotarsus and the posterolateral ridge of the tarsometatarsus.

In *Coccyzus erythrophthalmus* (Plates II, VII, X, XI, XIII) the gastrocnemius exhibits the same relationships and parts as in *Crotophaga*, although the fleshy belly extends only about halfway down the crus.

Pars externa arises by two heads. The larger head arises tendinous from the lateral surface of the external condyle of the femur and from the lateral surface of the distal arm of the biceps loop. The smaller head arises semitendinous from the posterior surface of the external condyle of the femur mesial to the biceps tendon and loop and unites with the lateral head about one-third the way down the crus. A little over halfway down the tibiotarsus the muscle gives way to a thin, broad tendon which joins those of the other two parts of this muscle.

Pars media arises semitendinous from the distomedial surface of the internal condyle and fleshy from the proximal surface of the internal condyle of the femur adjacent to the distal insertion of the accessorius semitendinosi and distomesial to the insertion of the adductor longus et brevis pars interna. The distal portion of the accessorius tendon is intimately fused with the posterior margin of the belly. This tendon continues distad to insert in part on the pars interna about 2 mm. distal to the insertion of the semimembranosus. The remainder continues down the medial aspect of the crus to fuse with the tendon of pars externa. This is the smallest of the three heads. The fleshy portion is triangular and about 7 mm. long; at its widest portion it is less than 3 mm.

Pars interna arises fleshy mostly from the mesial surface of the inner cnemial crest, but with a small medial aponeurosis arising from the patellar tendon. A small tendon passes down the posterior edge of the pars interna. This tendon is a direct continuation of the accessorius tendon and is joined to the tendon of the pars externa by an aponeurosis. About three-fourths the way down the tibiotarsus the tendon fuses with the tendon of the pars externa.

About one-fifth the way down the tibiotarsus the three main parts of this muscle are united by their tendons and aponeuroses to form a common mass enveloping the deeper muscles on the posterior aspect of the crus. The broad, flat common tendon passes superficially over the tibial cartilage to insert on the posterior surface of the hypotarsus and the posterolateral ridge of the tarsometatarsus.

In *Geococcyx californianus* (Plates XXVI, XXVII, XXIX) the gastrocnemius muscle (gastrocnemius—Shufeldt, 1886b: 473) is similar in most respects to that in *Crotophaga*.

Pars externa is composed of two heads. The larger lateral head arises by a tendon from the posterolateral surface of the external condyle of the femur and is intimately fused to the lateral surface of the distal arm of the biceps loop. The medial head has two distinct origins, both of which lie mesial to the biceps loop: a stout, flattened tendon from the intercondyloid region of the femur (Shufeldt described this as the *pars media*), and by a broad, flat aponeurosis from the posterior face of the external condyle. These two parts fuse about 15 mm. below their origin and the two heads fuse about 20 mm. below the head of the tibiotarsus.

Pars media arises by a short tendon from the distomesial surface and fleshy from the posterior face of the internal condyle of the femur. Proximally, the fibers are intimately fused with the insertion of the accessorius semitendinosi. The small (about 4 mm. wide and 20 mm. long) fleshy belly passes straight down the posteromesial side of the crus. The semitendinous band of the accessorius ligament crosses the proximal portion of the belly mesially. The distal continuation of the accessorius ligament crosses and fuses with the belly just below its midpoint. The resulting flat tendon passes down the proximal three-fourths of the mesial aspect of the crus. Shufeldt's description of this muscle is that of part of the medial head of the pars externa.

Pars interna arises mostly fleshy from the mesial surface of the inner cnemial crest and semitendinous from the mesial side of the patellar tendon. The pars interna and pars media are joined to the pars externa by fascia beginning just below the region of fusion of the former two parts. The conjoined Tendo Achillis passes over the posterior surface of the tibial cartilage to insert on the posterior surface of the hypotarsus and the posterolateral ridge of the tarsometatarsus.

The primary function of the gastrocnemius muscle is extension of the tarsometatarsus. There is an increase in the length of the belly in *Crotophaga* and *Geococcyx* over *Coc-*

cycus which seems to be associated with a more complete extension of the tarsometatarsus in the forward "pitch" of running in contrast to the constantly flexed condition in perching.

MUSCULUS PLANTARIS

This is a deeply situated fusiform muscle on the posterior aspect of the crus.

In *Crotophaga sulcirostris* (Plates XVIII, XIX, XX, XXV) the plantaris arises mostly fleshy from the posteromesial aspect of the proximal end of the tibiotarsus immediately below the internal articular surface and extending distal to the tibial insertion of the accessorius semitendinosi ligament. The fleshy, triangular belly is about 20 mm. long. Its thin tendon passes down the crus on the belly of the flexor digitorum longus muscle and inserts on the posteromesial corner of the proximal end of the tibial cartilage. The belly is crossed mesially by the tendon of insertion of the semimembranosus and by the short tibial branch of the ligament of the semitendinosus. It is bounded laterally by the flexor hallucis longus and the flexor perforatus digiti II muscles.

In *Coccyzus erythrophthalmus* (Plates V, VI, VII, VIII, XI, XIII) the plantaris muscle arises from a small area on the posteromesial aspect of the proximal end of the tibiotarsus immediately below the internal articular surface. The fleshy belly extends about halfway (20 mm.) down the tibiotarsus and then tapers into a thin tendon which inserts on the posteromesial corner of the proximal end of the tibial cartilage. Its relationships with other muscles are the same as in *Crotophaga*.

In *Geococcyx californianus* (Plates XXVII, XXIX) the plantaris muscle (soleus—Shufeldt, 1886b: 479) arises mostly fleshy on the posteromesial aspect of the head of the tibiotarsus. The small, triangular belly is about 30 mm. long. It tapers into a fine tendon which runs down the posteromesial surface of the tibiotarsus on the belly of the flexor digitorum longus, and inserts on the proximomesial corner of the tibial cartilage.

The M. plantaris aids in extension of the tarsometatarsus. The absolute length of the belly in *Coccyzus* equals the length in *Crotophaga* and exhibits a greater relative length to the length of the tibiotarsus than in either *Crotophaga* or *Geococcyx*.

MUSCULUS FLEXOR PERFORATUS DIGITI II

This muscle is one of three perforated flexor muscles situated on the posterior aspect of the crus under cover of the gastrocnemius muscle. The origin and bellies of these muscles are intimately related but their tendons are distinct and separate.

In *Crotophaga sulcirostris* (Plates XVI, XVII, XXI, XXII, XXV) this muscle is a direct continuation of the ambiens tendon. The belly is intimately fused with the flexor perforatus digiti III, flexor perforatus digiti IV and the flexor hallucis longus muscles and arises in part from the distal continuation of their common tendon of origin from the intercondyloid region of the femur. The tendon of flexor perforatus digiti II passes down the deep surface of the flexor perforatus digiti III. Its small tendon lies lateral to the tendon of flexor perforatus digiti IV and passes distad through the lateral side of the tibial cartilage. At the distal end of this cartilage the tendon turns sharply mesiad across the intertarsal joint deep to the tendons of Mm. flexores perforantes et perforati digiti II and III and the Mm. flexores perforati digiti III and IV. The tendon then passes through the proximal portion of the hypotarsus deep to the tendon of flexor perforans et perforatus digiti II and then continues downward along the mesial side of the hypotarsus and the tarsometatarsus. The tendon is perforated opposite the base of phalanx one of digit II by the tendon of flexor perforans et perforatus digiti II. The tendon of flexor perforatus digiti II inserts on the sides of the proximal phalanx of digit II. There is a continuous sheet of connective tissue enveloping the flexor tendons of the digits, however, so that only the main points of insertion may be determined with certainty.

In *Coccyzus erythrophthalmus* (Plates IV, V, IX, X, XIII) the flexor perforatus digiti II arises primarily as a continuation of the ambiens tendon and associated aponeuroses (see M. ambiens). This belly is intimately fused laterally with the Mm. flexores perforati digiti III and IV. The relationships of the tendon of the flexor perforatus digiti II in the tibial cartilage and the hypotarsus are the same as in *Crotophaga*. Opposite the base of the proximal phalanx of digit II the tendon is pierced by the tendon of the flexor

perforans et perforatus digiti II. The bifurcated tendon which results inserts laterally on both sides near the distal end of the proximal phalanx of digit II.

In *Geococcyx californianus* (Plates XXVI, XXIX) the flexor perforatus digiti II (flexor perforatus indicis primus pedis—Shufeldt, 1886b: 483) is distinctly biparite in form. The lateral head arises from the ambiens tendon. The medial head arises from the tendon of the flexor perforatus digiti III and is intimately fused with that muscle. The relationships of the tendon in the tibial cartilage and the hypotarsus are as in *Crotophaga*. The tendon inserts on the sides of the base of the proximal phalanx of digit II. This insertion is stout but short and is heaviest on the lateral side. As in the other genera, the tendon is perforated by the tendon of the flexor perforans et perforatus digiti II.

A strong fibrous band (annular ligament of Shufeldt) crosses the palmar surfaces of digits II and III. It is attached laterally near the base of the proximal phalanx of digit III and medially on the base of the proximal phalanx of digit II. This band holds the flexor tendons in place close to the bones and serves as an automatic flexor of the digits. From the fibrocartilaginous mass filling the external intertrochlear notch, a strong ligament runs distad to attach medially on the joint between phalanges one and two of digit IV and more or less completely ensheaths the tendon of flexor perforatus digiti IV. A similar band arising at the same place inserts in common with the palmar band on digit III, and a third ligament arises medially on the base of digit II and inserts medially on the base of the proximal phalanx of the hallux (See also automatic flexor of the hallux).

The flexor perforatus digiti II has similar features in all three genera, exhibiting no difference which might be of functional importance.

MUSCULUS FLEXOR PERFORATUS DIGITI III

In *Crotophaga sulcirostris* (Plates XIV, XV, XVI, XVII, XX, XXI, XXII, XXV) this muscle arises by a stout round tendon from the intercondyloid region of the femur in company with the flexor perforatus digiti IV and the flexor hallucis longus muscles. This tendon becomes flat and semitendinous and runs on the deep surface about three-fourths the length of the belly. It serves as an origin for some of the fibers of the flexor perforatus digiti II. The belly is intimately fused with the flexor perforatus digiti II, flexor perforatus digiti IV and the flexor hallucis longus and receives a semitendinous slip from the distal continuation of the ambiens tendon. The tendon passes superficially through the lateral side of the tibial cartilage and through the lateral groove of the hypotarsus but lies deep to and is grooved by the tendon of the flexor perforatus digiti IV. A short distance below the hypotarsus the tendon is joined by the long tendon of the peroneus longus muscle. It continues in a superficial position down the posterior sulcus of the tarsometatarsus and through the intertrochlear space. The tendon is pierced by the tendon of the flexor perforans et perforatus digiti III opposite the base of the proximal phalanx. The bifurcated tendon then inserts on the sides of phalanx one, on the proximal end of phalanx two and on the fibrocartilaginous pad between phalanges one and two.

No vinculum is present between the tendons of the flexor perforatus digiti III and the flexor perforans et perforatus digiti III.

In *Coccyzus erythrophthalmus* (Plates III, IV, V, VIII, IX, X, XIII) the flexor perforatus digiti III takes its origin primarily from a stout tendon arising from the intercondyloid region of the femur. This tendon also gives rise to the flexor hallucis longus and part of the flexor perforatus digiti IV. The belly also arises in part from a continuation of the ambiens tendon. The relationship of the tendon with the other flexor tendons in the tibial cartilage, hypotarsus and posterior sulcus of the tarsometatarsus is the same as in *Crotophaga*. The tendon of flexor perforatus digiti III is pierced by the tendon of the flexor perforans et perforatus digiti III about 2 mm. distal to the base of the proximal phalanx. The bifurcated tendon inserts on both sides of the distal end of the proximal phalanx, on the lateral side of the proximal end of phalanx two and on both sides of the pad between these two phalanges.

No vinculum is present between the tendons of the flexor perforatus digiti III and the flexor perforans et perforatus digiti III.

In *Geococcyx californianus* (Plates XXVI, XXIX) the flexor perforatus digiti III (flexor perforatus medius primus pedis—Shufeldt, 1886b: 483) is more distinctly bipar-

tite than in the other two genera. The larger head arises from a flat tendon from the intercondyloid region of the femur in common with the flexor perforatus digiti IV and the flexor hallucis longus and is intimately fused with these muscles. The smaller head arises from the continuation of the ambiens tendon and is intimately fused with the flexor perforatus digiti II. The two heads fuse about halfway down the crus. The relationship of the tendon in the tibial cartilage, the hypotarsus and the posterior sulcus is the same as in *Crotophaga*. Opposite the base of phalanx one of digit III, the tendon is perforated by the tendon of the flexor perforans et perforatus digiti III. Insertion is on the sides of the distal end of phalanx one, on the proximal end of phalanx two and on the pad between these phalanges.

No vinculum is present between the tendons of the flexor perforatus digiti III and the flexor perforans et perforatus digiti III.

I was unable to detect differences in the flexor perforatus digiti III among the three genera which would be of functional significance.

MUSCULUS FLEXOR PERFORATUS DIGITI IV

In *Crotophaga sulcirostris* (Plates XIV-XVI, XX-XXII, XXV) this muscle arises by a tendon from the intercondyloid region of the femur and from the ambiens tendon complex. This double origin gives the muscle a Y-shaped appearance. The proximal portion of the belly is intimately fused with the flexores perforati digiti II and III and the flexor hallucis longus muscles. Its small tendon lies superficial to the tendon of the flexor perforatus digiti III and grooves the latter in its course over the posterior surface of the tibial cartilage. The two tendons retain this relationship as they pass through the lateral groove of the hypotarsus. This is the most superficial tendon on the posterior aspect of the tarsometatarsus, lying directly under cover of the distal portion of the Tendo Achillis and associated connective tissue. The tendon does not ensheath the branch of the tendon of flexor digitorum longus which supplies digit IV. Insertion is on the lateral side (inner side of zygodactyl foot) of the proximal end of phalanx two of digit IV.

In *Coccyzus erythrophthalmus* (Plates II, III, IV, VIII, IX, X, XIII) the flexor perforatus digiti IV arises as in *Crotophaga* from the intercondyloid region of the femur and from the ambiens tendon. The relationship of its tendon to the other flexor tendons in the tibial cartilage, hypotarsus and the posterior sulcus of the tarsometatarsus is the same as in *Crotophaga*. The tendon does not ensheath the tendon of flexor digitorum longus supplying digit IV, but consists of a single discrete tendon which inserts laterally on the distal end of the proximal phalanx, on the proximal end of phalanx two and on the pad between these two phalanges.

In *Geococcyx californianus* (Plates XXVI, XXIX) the flexor perforatus digiti IV (flexor perforatus annularis primus pedis—Shufeldt, 1886b: 482) arises as in *Crotophaga* from the intercondyloid region of the femur and from the ambiens tendon complex. The relationship of its tendon to the other flexor tendons in the tibial cartilage, the hypotarsus and the posterior sulcus of the tarsometatarsus is the same as in *Crotophaga*. The tendon does not ensheath the tendon of the flexor digitorum longus muscle supplying digit IV. The tendon inserts on the lateral side of the base of phalanx two and on the pad between phalanges two and three of digit IV.

In the series *Coccyzus* to *Crotophaga* to *Geococcyx* there is a slight progressive reduction in the length of the fleshy belly of the flexor perforatus digiti IV. In other respects the muscle exhibits the same relationships among the three genera.

MUSCULUS FLEXOR PERFORANS ET PERFORATUS DIGITI II

This is one of two perforating and perforated flexor muscles situated on the posterolateral aspect of the crus. The proximal portion of both of these muscles is visible in a superficial view of the leg.

In *Crotophaga sulcirostris* (Plates XIV, XV, XVI, XXI, XXII, XXV) this muscle arises semitendinous from the external condyle of the femur and mostly fleshy from the distal arm and third arm of the biceps loop and from the patellar tendon. The small fleshy belly is about 14 mm. long, the proximal half being visible in a superficial view of

the leg. The long tendon passes down the posterior side of the crus under cover of the gastrocnemius muscle and through the mesial side of the tibial cartilage and the hypotarsus, and in the latter structure lies lateral to the tendon of the flexor perforatus digiti II. The tendon continues its course down the tarsometatarsus in a mesial position, and passes through the intertrochlear space deep to the tendon of the flexor perforatus digiti II and superficial to the tendon of the flexor digitorum longus. Opposite the base of the proximal phalanx of digit II the tendon pierces the tendon of the flexor perforatus digiti II and almost immediately is pierced by the branch of the tendon of flexor digitorum longus supplying digit II. The bifurcated tendon inserts on the sides of the proximal end of phalanx two and on the fibrocartilaginous pad between phalanges one and two of digit II.

In *Coccyzus erythrophthalmus* (Plates II, III, IV, IX, X, XIII) the flexor perforans et perforatus digiti II arises from the external condyle of the femur, the patellar tendon and the third arm of the biceps loop. It differs from *Crotophaga* in that its origin from the external condyle is less discrete and is shared by the flexores perforati digiti III and IV. This is a small triangular muscle, the belly being about 7 mm. long. The relationship of its tendon throughout the leg is the same as in *Crotophaga*. This tendon in *Coccyzus*, however, does not ensheath the tendon of the flexor digitorum longus muscle. The single tendon inserts mesially on the proximal end of the pad covering the joint between phalanges one and two of digit II.

In *Geococcyx californianus* (Plates XXVI, XXIX) the flexor perforans et perforatus digiti II (flexor perforatus indicis secundus pedis—Shufeldt, 1886b: 481) arises fleshy from the patellar tendon and the third arm of the biceps loop and arises by a stout tendon (shared with the flexor hallucis longus) from the posterolateral surface of the external condyle of the femur. The spindle-shaped belly is about 40 mm. long. Its tendon has the same relationship to the other flexor tendons as in *Crotophaga*. Opposite the base of the proximal phalanx of digit II, the tendon perforates the tendon of the flexor perforatus digiti II and about the middle of this phalanx is perforated by the tendon of the flexor digitorum longus muscle. It inserts on the sides of the distal end of phalanx one, on the proximal end of phalanx two and on the pad between phalanges one and two of digit II.

There is an increase in the length of the belly of flexor perforans et perforatus digiti II from *Coccyzus* to *Geococcyx*. This shift from a short, bulging head to a more slender belly appears to be correlated with the loss of grasping power but an increase in the extensibility and flexibility of the digits in *Geococcyx* over *Coccyzus*.

MUSCULUS FLEXOR PERFORANS ET PERFORATUS DIGITI III

In *Crotophaga sulcirostris* (Plates XIV, XV, XVI, XXI, XXII, XXV) the proximal third of this muscle is visible superficially. The fleshy belly extends about halfway down the crus. It arises fleshy from the third arm of the biceps loop, the patellar tendon, the outer cnemial crest, the lateral side of the head and shaft of the fibula and from the tendon of origin of the peroneus longus and peroneus brevis muscles. The belly is fused with the peroneus longus, the flexor digitorum longus and the flexor perforatus digiti IV muscles. Its tendon passes superficially through the tibial cartilage, taking a diagonal course from the outer upper side to the lower mesial side of the cartilage. The tendon is bounded laterally by the tendons of the flexores perforati digiti II, III, and IV. It passes through the medial groove of the hypotarsus lateral to the tendons of the flexor perforans et perforatus digiti II and the flexor perforatus digiti II. The tendon takes a diagonal course from mesial to lateral down the posterior sulcus of the tarsometatarsus, crossing over the tendon of the flexor perforatus digiti III, but is not connected with it by a vinculum. The tendon passes through the intertrochlear space immediately under the tendon of the flexor perforatus digiti III and pierces the latter tendon opposite the base of the proximal phalanx, and opposite the middle of phalanx two it is perforated by the tendon of the flexor digitorum longus. The bifurcated tendon inserts on the sides of the distal half of phalanx two, on the sides of the proximal end of phalanx three and on the fibrocartilaginous pad between these two phalanges of digit III.

In *Coccyzus erythrophthalmus* (Plates II, III, IV, IX, X, XIII) the flexor perforans et perforatus digiti III arises from the lateral surface of the head, shaft and spine of the fibula, from the lateral surface of the outer cnemial crest and from the tendon of origin of peroneus longus. It does not arise from the external condyle of the femur. The belly

extends about halfway down the tibiotarsus and is fused with the peroneus longus, flexor digitorum longus and the flexor perforatus digiti IV muscles. The relationship of its tendon in the tibial cartilage, hypotarsus and tarsometatarsus is the same as in *Crotophaga*. The tendon pierces the tendon of flexor perforatus digiti III about 2 mm. distal to the base of the proximal phalanx. Near the distal end of this phalanx it is pierced by the tendon of flexor digitorum longus. The latter tendon, however, is not fully exposed until about midway the length of phalanx two. The tendon of flexor perforans et perforatus digiti III inserts on the sides of the distal end of phalanx two and on the proximal end of phalanx three of digit III.

In *Geococcyx californianus* (Plates XXVI, XXVIII, XXIX) the flexor perforans et perforatus digiti III (flexor perforatus medius secundis pedis—Shufeldt, 1886b: 482) arises fleshy from the patellar tendon, by a flat tendinous band from the outer cnemial crest and semitendinous for a short distance (15 mm.) on the lateral surface of the spine of the fibula distal to the insertion of the biceps femoris. The proximal three-fourths of the belly is intimately fused with the peroneus longus muscle. The belly extends about halfway down the crus. The course and relationship of its tendon are the same as in *Crotophaga*. Opposite the base of phalanx one of digit III, the broad tendon perforates the tendon of flexor perforatus digiti III and opposite the middle of phalanx two is perforated by the tendon of the flexor digitorum longus. Insertion is primarily on the sides of the distal end of phalanx two, on the proximal end of phalanx three and on the pad between these two phalanges.

Because of the uniformity of development of this muscle among the three genera I was unable to find differences which could account for the mode of locomotion of these genera.

MUSCULUS FLEXOR DIGITORUM LONGUS

This is the most deeply situated muscle lying on the posterior aspect of the tibiotarsus. Its tendon trifurcates to supply digits II, III and IV.

In *Crotophaga sulcirostris* (Plates XVI, XVII, XVIII, XX, XXI, XXII, XXIII, XXV) the head of this muscle is bipartite and presents a Y-shaped appearance. It arises fleshy from the posterior face of the head, neck and spine of the fibula and from the proximal three-fifths of the posterior aspect of the tibiotarsus. The popliteus muscle lies deep to and between the two parts of the head of this muscle. Its tendon passes mesially through the deep surface of the tibial cartilage and through the medial canal of the hypotarsus. This tendon serves as the primary origin for the lumbricalis muscle and about two-thirds the way down the tarsometatarsus is joined by a long vinculum with the tendon of the flexor hallucis longus muscle. The tendon trifurcates a short distance above the distal end of the tarsometatarsus.

(1) Branch to digit II: This tendon perforates the tendon of the flexor perforans et perforatus digiti II opposite the middle of phalanx one. The main insertion is on the base of the ungual phalanx, but there is also a slip given off from the deep surface of the main tendon opposite the middle of phalanx two, and which inserts on the proximal end of the pad between phalanx two and the ungual phalanx.

(2) Branch to digit III: This tendon pierces the tendon of flexor perforans et perforatus digiti III opposite the middle of phalanx two. It inserts primarily on the base of the ungual phalanx, but, in addition, gives off the following slips from its deep surface: (a) one opposite the middle of phalanx two; inserts on the proximal end of the pad between phalanges two and three, (b) one opposite the middle of phalanx three; inserts near the distal end of phalanx three and on the pad between phalanx three and the ungual phalanx, (c) the smallest slip, given off near the distal end of phalanx three and which inserts on the proximal end of the pad between phalanx three and the ungual phalanx.

(3) Branch to digit IV: This tendon is not ensheathed by the tendon of the flexor perforatus digiti IV. The main point of insertion is on the base of the ungual phalanx, but the following discrete slips are given off from the deep surface of the main tendon: (a) one near the proximal end of phalanx two; inserts on the proximal end of the pad between phalanges two and three, (b) one near the distal end of phalanx three; inserts on the proximal end of the pad between phalanges three and four, (c) one near the proximal end of phalanx four; inserts on the distal end of phalanx four and on the pad between phalanx four and the ungual phalanx, (d) the smallest slip, given off opposite the distal

end of phalanx four, and which inserts on the proximal end of the pad between phalanx four and the ungual phalanx.

In *Coccyzus erythrophthalmus* (Plates III, IV, V, VI, VII, VIII, IX, X, XI, XIII) the flexor digitorum longus muscle arises from the proximal two-thirds of the posterior aspect of the tibiotarsus and from the posterior face of the head, shaft and spine of the fibula. In the proximal third, this belly is readily separated into two distinct heads giving the belly a Y-shaped appearance. The relationship of its tendon in the tibial cartilage and the hypotarsus is the same as in *Crotophaga*. About halfway down the tarsometatarsus its tendon is joined by a vinculum with the tendon of the flexor hallucis longus muscle. The lumbricalis muscle takes its origin from the tendons of both of these muscles. The tendon of the flexor digitorum longus trifurcates just proximal to the trochleae.

(1) Branch to digit II: This tendon is not ensheathed by the tendon of the flexor perforans et perforatus digiti II as it is in the other two genera. It inserts primarily on the proximal end of the ungual phalanx, but gives off from its under surface about a third the way down phalanx two a large slip which inserts on the distal end of phalanx two, and a smaller slip which inserts on the proximal end of the pad between phalanx two and the ungual phalanx.

(2) Branch to digit III: This tendon pierces the tendon of the flexor perforans et perforatus digiti III near the distal end of the proximal phalanx. It inserts primarily on the base of the ungual phalanx, but also sends off the following slips: (a) a slip near the middle of phalanx one, which inserts on the proximal end of the pad between phalanges one and two, (b) one near the middle of phalanx two, which inserts on the pad between phalanges two and three, (c) a large proximal and a small distal slip opposite phalanx three; the larger one inserts on the distal end of phalanx three and the smaller one inserts on the pad between phalanx three and the ungual phalanx.

(3) Branch to digit IV: This tendon is not ensheathed by the tendon of the flexor perforatus digiti IV muscle. The main insertion is on the base of the ungual phalanx, but four slips are given off of the main tendon opposite phalanges two, three and four as in *Crotophaga*.

In *Geococcyx californianus* (Plates XXVI, XXVII, XXIX) the flexor digitorum longus (flexor perforans digitorum profundus—Shufeldt, 1886b: 484) exhibits a more complicated origin than in the other genera. The tibial head arises from the posteromedial aspect of the tibiotarsus below the articular surface and extending a little over halfway (48 mm.) down that bone. The primary fibular head arises from the posterior surface of the head and body of the fibula. These two heads fuse about 5 mm. distal to the insertion of the biceps femoris. The secondary fibular head arises from the posterior surface of the spine of the fibula beginning immediately below the insertion of the biceps femoris tendon and from the posterior surface of the tibiotarsus extending to within 25 mm. of the distal end of that bone. Its stout tendon passes through the deep surface of the tibial cartilage mesial to the tendon of the flexor hallucis longus muscle and through the medial canal of the hypotarsus. The tendon then runs down the posterior sulcus of the tarsometatarsus deep to the tendon of the flexor hallucis longus muscle and is connected with that tendon by a short vinculum about 15 mm. above the distal end of the bone. The lumbricalis muscle arises from the tendon of the flexor digitorum longus muscle about halfway down the tarsometatarsus. The tendon trifurcates opposite the base of metatarsal I. Shufeldt stated that this tendon quadrifurcates, but this is incorrect. Shufeldt described only one of the accessory insertions of this tendon, namely, "to the underside of the shaft of the prebasal joint" of digit IV.

(1) Branch to digit II: This tendon perforates the tendon of flexor perforans et perforatus digiti II opposite the middle of the proximal phalanx. The main point of insertion is on the base of the ungual phalanx, but the tendon also gives off the following discrete slips from its deep surface: (a) one near the middle of phalanx one, which inserts on the pad between phalanges one and two, (b) one near the middle of phalanx two, which inserts on the distal end of that phalanx, (c) one near the distal end of phalanx two, which inserts on the pad between phalanx two and the ungual phalanx.

(2) Branch to digit III: This tendon perforates the tendon of the flexor perforans et perforatus digiti III muscle opposite the middle of phalanx three. The primary inser-

tion is on the base of the ungual phalanx, but it also gives off three smaller slips as in *Crotophaga*.

(3) Branch to digit IV: This tendon is not ensheathed by the tendon of the flexor perforatus digiti IV. It inserts primarily on the base of the ungual phalanx, but also gives off four smaller slips as in *Crotophaga*.

As is true of the other flexor muscles of the digits, the flexor digitorum longus muscle exhibits a uniformity of development among the three genera. Certain minor differences probably are not important functionally. There is a progressive decrease in the area of origin of the muscle in the series *Coccyzus*, *Crotophaga*, *Geococcyx*, but the overall length of the fleshy fibers is relatively the same in the three genera. Inasmuch as the main point of insertion of its tendon is on the ungual phalanx of digits II, III and IV, contraction of the muscle results in a strong flexion of the terminal phalanx of these digits. This flexion probably is important both for grasping a branch, as in *Coccyzus*, and in the "pitch-off" in running, as in *Geococcyx*.

MUSCULUS FLEXOR HALLUCIS LONGUS

This is a long muscle lying between the flexor digitorum longus and the more superficial flexors of the digits. It arises on the femur and inserts on the ungual phalanx of the hallux.

In *Crotophaga sulcirostris* (Plates XVI, XVII, XVIII, XXI, XXII, XXV) this muscle arises from the intercondyloid region of the femur by a stout tendon shared with the flexores perforati digiti III and IV, and fleshy from the posterior face of the external condyle of the femur. The belly extends about halfway down the crus and is intimately fused proximally with the flexores perforati digiti II, III, and IV. Its tendon passes laterally through the deep surface of the tibial cartilage and through the lateral canal of the hypotarsus. The tendon crosses over the tendon of flexor digitorum longus to the mesial side of the tarsometatarsus, and about two-thirds the way down that bone the two tendons are joined by a long vinculum. The greater part of the lumbricalis muscle takes origin from the tendon of flexor digitorum longus, only a few fibers arising from the tendon of flexor hallucis longus. Opposite the base of the proximal phalanx of the hallux the tendon is ensheathed by the tendon of the flexor hallucis brevis muscle. The main point of insertion is on the proximal end of the ungual phalanx, but there is also a small slip given off to insert on the fibrocartilaginous pad between the proximal and ungual phalanges of the hallux.

The automatic flexor of the hallux is a strong ligament which arises from the wing of the trochlea for digit IV and the fibrocartilaginous mass filling the external intertrochlear notch. This ligament passes mesiad across the intertrochlear space to the palmar surface of the hallux superficial to the tendons of flexor hallucis brevis and flexor hallucis longus. Near the distal end of phalanx one the ligament passes to the mesial side of the tendon of the flexor hallucis longus to insert on the pad between the proximal and ungual phalanges.

In *Coccyzus erythrophthalmus* (Plates IV, V, VI, IX, X, XIII) the flexor hallucis longus muscle arises from the intercondyloid region and the posterior face of the external condyle of the femur as in *Crotophaga*. About one-fourth the way down the tibiotarsus, the belly gives way to a small tendon which continues distad between flexor digitorum longus and flexor perforatus digiti II. The relationship of its tendon to other tendons in the tibial cartilage and the hypotarsus are the same as in *Crotophaga*. The tendon passes from lateral to mesial over the tendon of flexor digitorum longus and is united with it by a vinculum about three-fourths the way down the tarsometatarsus. Its tendon passes lateral to the first metatarsal in company with the tendon of the flexor hallucis brevis and is completely ensheathed by the expanded tendon of the latter muscle. The tendon of flexor hallucis longus pierces this sheath opposite the proximal end of phalanx one and continues distad to insert on the proximal end of the ungual phalanx. A slip is given off from the deep surface of this tendon and inserts with the automatic flexor ligament on the pad between the two phalanges of the hallux.

The automatic flexor of the hallux has the same relationships as in *Crotophaga*.

In *Geococcyx californianus* (Plates XXVI, XXIX) the flexor hallucis longus muscle (flexor longus hallucis—Shufeldt, 1886b: 483) also arises from the intercondyloid region

and the posterior face of the external condyle of the femur. Its tendon arises near the midline of the belly and exhibits the same relationships in the tibial cartilage and the hypotarsus as in the other two genera. The tendon crosses over the tendon of the flexor digitorum longus muscle and is united with it by a short (3 mm. long) vinculum about 15 mm. from the distal end of the tarsometatarsus. At the distal end of that bone the tendon of flexor hallucis longus is ensheathed by the tendon of the flexor hallucis brevis muscle. The primary point of insertion is on the base of the ungual phalanx but it also gives off from its deep surface a slip which inserts on the pad between the proximal and ungual phalanges.

The automatic flexor ligament of the hallux is well developed and exhibits the same relationships as in the other genera. There is also a fibrous band arising from the trochlea for digit IV and which is attached to the proximolateral surface of the first phalanx of the hallux. Shufeldt did not describe the automatic flexor ligament nor the double insertion of the tendon of flexor hallucis longus.

MUSCULUS POPLITEUS

This is the deepest muscle on the posterior aspect of the crus and is visible only after removal of the flexor digitorum longus muscle.

In *Crotophaga sulcirostris* (Plate XXV) this muscle is fleshy and well developed. It arises from the posteromesial surface of the head and neck of the fibula. The fibers pass distomesiad to insert on a diagonal line on the posterior aspect of the tibiotarsus. The total length of this muscle is 2 mm.; it is about 5 mm. wide at its origin and 3 mm. wide at its insertion.

In *Coccyzus erythrophthalmus* (Plate XIII) the popliteus muscle is about 2 mm. in length and 2 mm. in width. It arises from the posteromesial aspect of the head and neck of the fibula and its fibers pass distomesiad to insert on a diagonal line on the posterior surface of the tibiotarsus slightly distal to the point of origin.

In *Geococcyx californianus* (Plates XXVI, XXIX) the popliteus muscle (popliteus—Shufeldt, 1886b: 485) arises semitendinous from the mesial surface of the head and neck of the fibula for a distance of about 7 mm. It inserts partly semitendinous on the posterior surface of the tibiotarsus opposite the origin of the muscle. Shufeldt gave the fibular attachment as the insertion for this muscle.

MUSCULUS EXTENSOR HALLUCIS LONGUS

This muscle is situated on the anteromesial aspect of the tarsometatarsus.

In *Crotophaga sulcirostris* (Plates XV, XVII, XIX, XXI, XXIII, XXIV) this muscle arises from the anteromesial aspect of the proximal end of the tarsometatarsus extending about two-thirds (20 mm.) the distance down the shaft. The lateral fibers arise from the tendon of the extensor proprius digiti III muscle and the distal portion of the origin consists of scattered muscle bundles. Its tendon passes to the lateral side of the bone about two-thirds the way down the shaft and under a heavy, fibrous band on the first metatarsal. The tendon then expands and runs down the dorsolateral surface of the hallux to insert on the base of the ungual phalanx. The tendon of the extensor digitorum longus muscle passes between the belly of the extensor hallucis longus muscle and the tendon of tibialis anticus.

An automatic extensor ligament of the claw of the hallux arises on the dorsomesial surface of the proximal phalanx and inserts on the base of the ungual phalanx ventral to the tendon of the extensor hallucis longus. Similar automatic extensors have been described for other birds by Hudson (1937: 50) and Richardson (1942: 348).

In *Coccyzus erythrophthalmus* (Plates VI, VII, IX, XI, XII) the extensor hallucis longus muscle arises fleshy from the anteromesial side of the proximal end of the tarsometatarsus and for a distance of about 10 mm. down the shaft of that bone. Its tendon passes obliquely down the bone and under a heavy sheath on the first metatarsal. The tendon inserts on the base of the ungual phalanx.

An automatic extensor ligament of the claw arises from the dorsomesial surface of the proximal phalanx and inserts on the base of the ungual phalanx.

In *Geococcyx californianus* (Plates XXVII, XXVIII) the extensor hallucis longus muscle (extensor brevis digitorum, in part—Shufeldt, 1886b: 480-481) arises on the anteromesial surface of the tarsometatarsus for a distance of about 28 mm. Its tendon passes under a heavy, fibrous band on metatarsal I and then continues along the extensor surface of the proximal phalanx of the hallux to insert dorsolaterally on the base of the ungual phalanx.

A well developed automatic extensor ligament of the claw arises about midway the length of the proximal phalanx and inserts on the proximal end of the ungual phalanx. Shufeldt did not describe this ligament.

Shufeldt described four distinct and separate muscles under the name Extensor brevis digitorum. These are M. extensor hallucis longus, M. extensor proprius digiti III, M. extensor brevis digiti IV, and M. abductor digiti II.

MUSCULUS EXTENSOR PROPRIUS DIGITI III

This muscle lies on the anterior surface of the tarsometatarsus between the extensor hallucis longus and the extensor brevis digiti IV muscles and directly under the tendon of M. extensor digitorum longus.

In *Crotophaga sulcirostris* (Plates XV, XIX, XX, XXI, XXIII, XXIV) this muscle arises semitendinous for a distance of about 9 mm. on the anterior surface of the tarsometatarsus beginning about 2 mm. distal to the insertion of the tibialis anticus tendon and arises by fleshy fibers extending to the distal foramen. Its belly is partly fused with the extensor brevis digiti IV and the extensor hallucis longus muscles. Its short broad tendon (about 1 mm. in length and width) inserts on the dorsomesial surface of the base of the proximal phalanx of digit III.

In *Coccyzus erythrophthalmus* (Plates III, VII, VIII, IX, XI, XII) the extensor proprius digiti III arises by fleshy fibers from the anteromesial ridge of the tarsometatarsus from the point of insertion of the tibialis anticus tendon to within 4 mm. of the trochlea for digit IV. Its tendon receives on both sides a mass of fan-like fibers arising from the distal third of the bone. These fleshy fibers accompany the tendon almost to its insertion on the dorsal surface of the base of the proximal phalanx of digit III.

In *Geococcyx californianus* (Plates XXVII, XXVIII) the extensor proprius digiti III muscle (extensor brevis digitorum, in part—Shufeldt, 1886b: 481) is short and bulky. It arises fleshy from the distal third of the anterior surface of the tarsometatarsus, and its belly increases in size as it passes distad. Its broad tendon inserts on the dorsal surface of the base of the proximal phalanx of digit III.

There is a progressive decrease in length but increase in bulk of the fleshy fibers of the extensor proprius digiti III from *Coccyzus* to *Crotophaga* to *Geococcyx*.

MUSCULUS EXTENSOR BREVIS DIGITI IV

This muscle is situated on the anterolateral aspect of the tarsometatarsus and is bounded mesially by the extensor proprius digiti III muscle, with which it is in intimate contact throughout its fleshy portion.

In *Crotophaga sulcirostris* (Plates XIV, XIX, XXI, XXII, XXIV) this muscle arises from the anterolateral aspect of the tarsometatarsus extending from just below the head of that bone to within 6 mm. of the trochlea for digit IV. The fleshy fibers accompany the tendon to the base of the trochlea. Its short (about 4 mm.), stout tendon passes through a groove on the mesial surface of the trochlea for digit IV and inserts on the mesial side of the base of the proximal phalanx of digit IV.

In *Coccyzus erythrophthalmus* (Plates II, IX, X, XII) the extensor brevis digiti IV muscle arises from the anterolateral aspect of the tarsometatarsus extending from the proximal end of that bone to within 4 mm. of the external intertrochlear notch. The stout tendon, 3 mm. long, passes through the external intertrochlear notch mesial to the trochlea for digit IV and inserts on the mesial side of the base of the proximal phalanx of digit IV. Hudson (1937: 54) has pointed out that in *Coccyzus americanus* its tendon does not pass under a bony bridge. This is true also for *C. erythrophthalmus*, *Crotophaga* and *Geococcyx*.

In *Geococcyx californianus* (Plates XXVI, XXVII, XXVIII) the extensor brevis digiti IV (extensor brevis digitorum, in part—Shufeldt, 1886b: 481) arises on the anterolateral aspect of the tarsometatarsus beginning about 2 mm. below the head and extending to within 6 mm. of the distal end of the trochlea for digit IV. The proximal three-fourths of the muscle are flat, the distal one-fourth is round. Its round tendon passes along the groove on the mesial surface of the trochlea to insert on the ventromedial surface of the base of the proximal phalanx of digit IV.

The belly of the extensor brevis digiti IV muscle appears to be slightly less well developed in *Geococcyx* than in the other two genera, but the difference is probably not important for locomotion.

MUSCULUS ABDUCTOR DIGITI II

This small muscle lies on the anteromesial aspect of the tarsometatarsus between the belly of the extensor proprius digiti III and the tendon of the extensor hallucis longus muscle.

In *Crotophaga sulcirostris* (Plates XIX, XX, XXI, XXIII, XXIV) this muscle arises fleshy from the distal end of the anteromedial ridge of the tarsometatarsus beginning about 15 mm. proximal to the internal intertrochlear notch and extending to the mesial surface of the trochlea for digit II. The belly is in intimate contact laterally with the extensor proprius digiti III; the proximal portion of its belly is hidden by the extensor hallucis longus muscle. None of its origin takes place from metatarsal I. Its short thin tendon runs distad over the mesial surface of the trochlea for digit II and inserts mesially on the base of the proximal phalanx of digit II.

In *Coccyzus erythrophthalmus* (Plates VII, VIII, IX, XI, XII) the abductor digiti II arises along a long narrow line on the anteromesial ridge of the tarsometatarsus beginning about 8 mm. below the proximal end of that bone and extending to the proximal end of the trochlea for digit II. Its short stout tendon passes mesially around the trochlea and inserts on the mesial side of the base of the proximal phalanx of digit II.

In *Geococcyx californianus* (Plates XXVII, XXVIII) the abductor digiti II muscle (extensor brevis digitorum, in part—Shufeldt 1886b: 481) arises from the anteromesial aspect of the distal one-fourth of the tarsometatarsus. Its very thin tendon inserts mesially about 2 mm. from the base of the proximal phalanx of digit II.

There is a progressive decrease in the length of the belly of the abductor digiti II muscle from *Coccyzus* to *Crotophaga* to *Geococcyx*. It seems possible that abduction of digit II is more important for perching than for running.

MUSCULUS FLEXOR HALLUCIS BREVIS

This muscle lies on the posteromesial aspect of the tarsometatarsus.

In *Crotophaga sulcirostris* (Plates XVI, XIX, XX, XXI, XXII, XXIII, XXV) the flexor hallucis brevis muscle arises by fleshy fibers from the mesial and ventral surfaces of the hypotarsus and from the posteromesial surface of the tarsometatarsus extending distal from the head of that bone for about 20 mm. Its long band-shaped tendon arises on the posterior surface of the distal half of the belly. The tendon widens to ensheath the tendon of the flexor hallucis longus opposite the base of the first phalanx of the hallux. The tendon inserts on both sides of the proximal end of phalanx one of the hallux.

In *Coccyzus erythrophthalmus* (Plates IV, V, VII, VIII, IX, X, XI, XIII) the flexor hallucis brevis muscle arises from the mesial surface of the hypotarsus and from a small area (about 14 mm. in length) from the posteromesial aspect of the proximal end of the tarsometatarsus. Its strong flat tendon passes down the posteromesial aspect of the bone in a superficial position, passes lateral to metatarsal I where it becomes an enlarged fibrocartilaginous sheath which encloses the tendon of the flexor hallucis longus muscle. The latter tendon perforates this sheath opposite the proximal end of phalanx one and the resulting split tendon of the flexor hallucis brevis then inserts on the mesial and lateral sides of the proximal phalanx of the hallux.

In *Geococcyx californianus* (Plates XXVI, XXVII, XXIX) the flexor hallucis brevis muscle (flexor brevis hallucis—Shufeldt, 1886b: 485) arises by fleshy fibers from

the mesial and ventral surfaces of the hypotarsus and from the posteromesial sulcus of the tarsometatarsus for a distance of about 20 mm. The tendon enlarges opposite metatarsal I to ensheath the tendon of flexor hallucis longus. Shufeldt did not mention the sheath-like nature of this tendon. The tendon inserts primarily on the lateral side of the base of the proximal phalanx.

There is a progressive reduction in the length of the belly of the flexor hallucis brevis muscle from *Coccyzus* to *Geococcyx*. This trend would seem to indicate less need for flexion of the proximal phalanx of the hallux in *Geococcyx* as compared with *Coccyzus*.

MUSCULUS ADDUCTOR DIGITI II

This is the smallest muscle in the lower leg and is situated deep in the posterior sulcus of the tarsometatarsus between the flexor hallucis brevis and the abductor digiti IV muscles.

In *Crotophaga sulcirostris* (Plates XXI, XXII, XXV) the adductor digiti II muscle arises by fleshy fibers from the midline of the ventral surface of the hypotarsus and from the posterior surface of the tarsometatarsus for a distance of 2 mm. distal to the hypotarsus. The belly, which is about 8 mm. in length, is fused laterally with the abductor digiti IV muscle. Its long thin tendon passes down the posterior sulcus close to the bone and through the internal intertrochlear notch to insert laterally on the base of the proximal phalanx of digit II.

In *Coccyzus erythrophthalmus* (Plates IX, X, XIII) the adductor digiti II muscle arises from the ventral surface of the hypotarsus and from the posterior surface of the tarsometatarsus immediately below the hypotarsus. This fleshy belly is about 2.5 mm. in length. Its very fine tendon (about 0.2 mm. in width) passes obliquely distad under cover of flexor hallucis brevis to the medial ridge of the tarsometatarsus. The tendon then goes through the internal intertrochlear notch, where it begins to widen, so that at its point of insertion on the lateral side of the proximal end of phalanx one of digit II it is about 0.7 mm. in width.

In *Geococcyx californianus* (Plates XXVI, XXIX) the adductor digiti II muscle (not described by Shufeldt) is a minute muscle about 1 mm. in width at its origin. It arises from the ventral midline of the hypotarsus and the tarsometatarsus directly below for a distance of about 8 mm. At the latter point, a hair-like tendon passes diagonally down the bone, through the internal intertrochlear notch to insert laterally on the base of the proximal phalanx of digit II.

MUSCULUS LUMBRICALIS

This is a deeply situated muscle in the posterior sulcus of the tarsometatarsus and which arises primarily from the tendon of flexor digitorum longus muscle and inserts on fibrocartilaginous pads between the trochleae and the proximal phalanges of the digits.

In *Crotophaga sulcirostris* the lumbricalis muscle arises by fleshy fibers primarily from the lateral side of the tendon of flexor digitorum longus beginning about 3 mm. below the hypotarsus, but arises in part from the tendon of the flexor hallucis longus muscle beginning about 8 mm. below the hypotarsus. The fleshy fibers pass down the lateral and anterior surfaces of the tendon of the flexor digitorum longus and insert mostly by fleshy fibers on the joint pulley for digit III and by semitendinous fibers on the joint pulley for digit IV.

In *Coccyzus erythrophthalmus* the lumbricalis muscle also arises primarily from the tendon of the flexor digitorum longus muscle beginning about 3 mm. below the hypotarsus. The belly increases in size distally and receives a few fibers from the tendon of the flexor hallucis longus muscle. The lumbricalis muscle envelops the tendon of flexor digitorum longus except on its posterior surface. The muscle bifurcates at about the level of the proximal end of metatarsal I. Both branches become slightly tendinous. The mesial branch passes deep to the trifurcated tendon of flexor digitorum longus and inserts on the proximal end of the joint pulleys of digits II and III. The lateral branch runs laterad to the tendons of flexor digitorum longus and inserts laterally on the proximal end of the joint pulley for digit IV.

In *Geococcyx californianus* the lumbricalis muscle is less well developed than in the other genera. It arises solely from the tendon of the flexor digitorum longus beginning about 20 mm. distal to the hypotarsus. The muscle passes down the anterior and lateral sides of the tendon of flexor digitorum longus to insert as a solid sheet of fleshy fibers on the joint pulley for digit III, to a slight extent laterally on the joint pulley for digit II, and semitendinous on the lateral side of the joint pulley for digit IV. Shufeldt did not describe this muscle.

Hudson (1937: 57) had the following to say regarding the lumbricalis: "Meckel (vide Gadow—1891, p. 204) considered this muscle as serving to draw the joint pulley behind in order to protect it from pinching during the bending of the toes. It perhaps also tends to flex the third and fourth digits."

MUSCULUS ABDUCTOR DIGITI IV

This muscle lies in a superficial position on the posterolateral aspect of the tarsometatarsus.

In *Crotophaga sulcirostris* (Plates XIV, XV, XXI, XXII, XXV) this muscle arises by fleshy fibers from the distolateral corner of the tibial cartilage, the lateral surface of the hypotarsus and from the posterolateral aspect of the tarsometatarsus extending from the head of that bone to within 6 mm. of the trochlea for digit IV. The origin of the distal portion of the belly consists of widely spaced muscle strands. The proximal portion of the belly of the muscle is crossed superficially in a diagonal direction by the long tendon of the peroneus longus muscle. Its tendon forms about one-third the way down the tarsometatarsus and passes distad on the posterolateral surface of that bone in close proximity to the tendon of the flexor digitorum longus muscle. The tendon passes under a heavy, fibrous band on the base of the trochlea for digit IV and inserts laterally on the base of the proximal phalanx of digit IV.

In *Coccyzus erythrophthalmus* (Plates II III, IX, X, XIII) the abductor digiti IV muscle arises from the same areas as in *Crotophaga*, though its belly is relatively shorter. Its tendon passes under a fibrous band on the base of the trochlea for digit IV and inserts on the lateral side of the base of the proximal phalanx of digit IV.

In *Geococcyx californianus* (Plates XXVI, XXIX) the abductor digiti IV muscle (extensor brevis annularis—Shufeldt, 1886b: 485) also arises from the distolateral corner of the tibial cartilage and associated fascia, the lateral surface of the hypotarsus and from the posterolateral aspect of the tarsometatarsus. The belly is about 20 mm. in length, but as in the other two genera, scattered muscle bundles arise to within 15 mm. of the distal end of the tarsometatarsus. Its tendon passes under a sheath on the base of the trochlea for digit IV and inserts laterally on the base of the proximal phalanx. Shufeldt overlooked the origin from the tibial cartilage.

No functionally important differences could be found among the three genera in the abductor digiti IV muscle.

MUSCULUS ADDUCTOR DIGITI IV

This muscle was originally described in the *Rhea* by Gadow. It has since been described by Hudson (in *Phasianus colchicus torquatus*, 1937: 58) and by Wilcox (in *Gavia immer*, 1948: 67-68).

What might be considered a vestige of this muscle in *Crotophaga sulcirostris* is present in the form of a short, fibrous band, about 2 mm. long and 0.5 mm. wide, which arises from the posterior aspect of the tarsometatarsus immediately below the facet for metatarsal I. It attaches to the proximal end of the joint pulley for digit III deep to the point of insertion of the lumbricalis muscle.

I was unable to demonstrate the presence of such a muscle or its vestige in *Coccyzus erythrophthalmus*, even with 20 \times magnification.

Shufeldt did not describe the adductor digiti IV muscle in *Geococcyx californianus*. I found only a fibrous band showing the same form and relationship as in *Crotophaga*.

Discussion

REVIEW OF THE LOCOMOTOR HABITS OF THE THREE GENERA

The members of the genus *Coccyzus* are arboreal birds. Bent (1940: 62)

said that "the flight of the cuckoo is rather swift, easy and graceful, exceedingly direct and horizontal, but turning frequently from side to side as it threads its way through the branches of the trees." Both Yellow-billed and Black-billed Cuckoos inhabit thickets and the understory of mixed woods, but occasionally are found in the crown of climax Beech-Maple forests, although their nests are almost invariably placed in tangles or in saplings. They are not inhabitants of dense woods. Eaton (1914, vol 2: 132) said of the Yellow-billed Cuckoo that "its call is heard from the copses, hedgerows, orchards, swampy thickets and vine-clad hillsides which it chooses to inhabit." Forbush (1927, vol. 2: 246) stated that the two species "are almost identical in appearance and habits and they haunt the same places." I have never seen a cuckoo on the ground. The only reference to their mode of locomotion when on the ground is that of Engels (1938: 210) who stated that "It seldom comes down to the ground; when it does so, it is said to be uncommonly awkward or clumsy in its hopping." Forbush (op. cit., p. 247) reported that "The Black-billed Cuckoo seems more inclined to go to the ground than is the other species, though it is rather seldom seen there." My captive Yellow-billed Cuckoo hopped awkwardly when on the bottom of its cage. Limitations in cage size, however, may have affected the manner of locomotion on a flat surface.

Coues (1903, vol. 2: 603) said that the *Crotophaginae* are terrestrial. In a study of the Smooth-billed Ani (*Crotophaga ani*) Davis (1940: 196) stated that "The birds are awkward in all movements. They walk with a peculiar disjointed gait and sometimes run a few feet; on the ground they seldom hop. In flight the bird flaps and soars alternately and when landing in a tree, the wings and tail are uncontrolled. . . . The birds feed almost entirely on the ground." Bent (1940: 33) had the following to say regarding the Groove-billed Ani: "Mr. Skutch writes (MS.): 'Their flight is as perfectly characteristic of the birds as any other of their peculiar habits. A long journey, say anything much in excess of a hundred yards, is seldom made by a continuous flight, but the bird advances with frequent pauses in conveniently situated trees and bushes.'"

Coues (1903, vol. 2: 605) spoke of the genus *Geococcyx* as being "Eminently terrestrial." Sutton (in Bent, 1940: 38) said that "The speed of the roadrunner is remarkable. Not when he is flying—a flying roadrunner is as much out of his element as a swimming chicken—but when he is afoot." A further insight into the behavior of these birds was given by the same author (p. 37): "Watch him race across the sand, full speed, after a lizard. Watch him put out a wing, change his course, throw up his tail, change his course again, plunge headlong into a clump of cactus, and emerge, whacking his limp victim on the ground. . . . Watch him stalk a grasshopper, slipping quietly forward, making a sudden rush with wings and tail fully spread, frightening the doomed insect into flight, then leaping 3 or 4 feet in air to snatch it flycatcherwise in his long bill." Cottam et al. (1942: 131) reported a running speed of 12 to 15 miles per hour for the road-runner.

COMPARISON OF MUSCLE VARIATIONS WITH DIFFERENCES IN
HABITS AND LIMB PROPORTIONS

It has been assumed by Larson (1930: 409) and Engels (1938: 207) that the road-runner has been derived from an arboreal ancestor. The best evidence for this assumption in the Cuculidae is zygodactylism. This foot condition is not found in any other terrestrial birds. The extreme differences in habits between the arboreal cuckoo and the cursorial road-runner would lead one to expect pronounced adaptive differences in the anatomy of these birds. Similarly, one would expect to find the structure of the ani to be intermediate between these two genera. These anticipated differences are readily seen with respect to skeletal-limb proportions discussed above (pp. 523-526). It is a well established principle of comparative anatomy that in closely related forms cursorial animals possess longer appendages than non-cursorial animals. This has been shown to be true for *Geococcyx* as compared to *Coccyzus* (p. 524, and Engels, 1938). The principle that the distal elements of appendages respond more quickly in adaptive changes than do proximal elements also has been demonstrated (pp. 524-526; Miller, 1937: 46; Engels, 1938: 212).

Questions arise concerning the myological changes accompanying these changes in skeletal proportions. Mere increase in length of limb bones requires only a similar increase in the length of the belly or tendon of the muscle associated with those bones. Differences in the form or relative development of the muscles themselves are not necessary unless differences in the habits of the bird necessitate them.

Before entering upon a discussion of this problem it seems desirable to mention certain factors pertaining to locomotion in a bipedal animal. The development of bipedalism in animals which have not assumed the fully erect posture makes it necessary to balance the preacetabular portion of the body by post-acetabular structures: the tail in bipedal dinosaurs (Romer, 1946: 211), or back-thigh muscles in the proavians (Böker, 1935: 106-108), and in birds. Stolpe (1932) discussed in detail the basic construction of the pelvic girdle and leg in birds with respect to locomotion. He emphasized the importance of maintaining the center of gravity of the bird above the supporting leg during the walking movement. The displacement of the center of gravity in some birds is effected by the lateral inclination of the supporting leg and by rotation of the longitudinal axis of the body. Concomitant with these compensations, stabilization of the pelvic girdle in alternate leg action is necessary.

Miller (1937: 20-22) discussed the movement of the limb segments in locomotion in geese. During the walking movement in geese the unsupported side of the body is tossed upward and the fall is caught on the foot of that side in fully protracted position. The forward axis, likewise, is tossed to the left in making a step with the right foot, and to the right for the step with the left. The road-runner has a smoother gait, and the mechanism for that is sought here.

Howell (1926: 173-216) discussed the difficulty of determining the individual actions of muscles. In attempting to analyze the muscles of a bird's leg this difficulty is great because of the fusion of the bellies and of the com-

plexity of the origins and insertions of many of them. Certain muscles, therefore, must be treated as members of complexes rather than as individuals. The simple action of some individual muscles, however, may be determined even though these muscles may perform different actions on different bones or joints.

In considering the functional anatomy of the muscles of a running bird in contrast to that of a perching bird, the muscles acting between the axis and the femur are of greatest interest. A perching bird ordinarily supports its weight on the two legs simultaneously, while a running bird supports its weight alternately on first one leg and then the other. The perching bird, therefore, by bilateral action of muscles can maintain passive balance in all respects except pitch of the vertebral axis in the sagittal plane. The running bird, on the other hand, because of unilateral action of muscles must maintain dynamic balance in three planes against pitch, roll and swing of the axis.

The fundamental sets of simple movements by pairs of antagonists on a femur flexibly attached to a fixed axis are: (1) protraction and retraction; (2) abduction and adduction; (3) medial and lateral rotation. These simple movements are modified in a running bird by the fact that the leg and not the axis is fixed during its retraction; the leg, therefore, must balance a movable axis on the acetabulum as a fulcrum. Thus the corollaries of the three sets of movements listed above are: (1) pitch of the axis in the midsagittal plane; (2) roll of the axis in the transverse plane; (3) swing of the axis in the frontal plane.

Some muscles pull at an angle to the line or plane of movement of their points of insertion. Their pulls, therefore, may be resolved into two or more components. Let us consider a muscle originating on a median axial structure, such as the pygostyle, mesial, caudal and dorsal to its point of insertion, such as the midpoint of the shaft of the left femur. Such a muscle would pull at an angle to each of the three planes of trunk movement and would produce three components: (1) retract the femur or pitch the foreaxis upward; (2) roll the axis to the left (ventrad); (3) swing the foreaxis to the right. Of these three components the first is functionally desirable but the last two are undesirable in locomotion. The last two can be reduced by shifting the point of origin of the muscle laterad into the plane passing through the fulcrum and its point of insertion. Running consists of a series of falls forward by the axis and of partial recoveries by the alternately protracted legs, speed being inversely related to the completeness of recovery. Smooth running with the axis pointed and held in the straight line of progression requires a nicely balanced system of forces, levers, fulcra and directions of application. Since a balance between pitch and fall of the foreaxis must be maintained during femoral retraction (or axial propulsion) the angle of the muscle with reference to the plane passing through the fulcrum and its point of insertion is important. Pitch can be reduced to balance fall by forward movement of the point of origin of the muscle.

The ilirotrochantericus anticus and ilirotrochantericus posticus muscles protract the femur and rotate its lateral surface forward. The progressive caudal shift from *Coccyzus* to *Geococcyx* of the fleshy origin of the posticus,

however, indicates that in *Geococcyx* abduction in this muscle probably is as important as are protraction and rotation. Stolpe (1932: 178, 242) stated that abduction and adduction of the femur are made impossible by the relationship of the head and neck of the femur to the antitrochanter and by the form of the synovial capsule and the ligamentum teres. These factors aid in fixing the angle between the femur and frontal plane. When the foot is fixed on the ground during contraction of the ilirotrochantericus posticus muscle, its result becomes that of supporting the axis against roll induced by contraction of the muscle of the other leg. The ilirotrochantericus anticus muscle is more strongly developed in *Crotophaga* and *Geococcyx* than in *Coccyzus*, although its form indicates that it has a greater range of contraction in the last genus. Greater range in turn implies greater rotation of the femur in *Coccyzus* and shorter range in the other genera implies relative fixation in them of the fronto-femoral angle.

The iliobtibialis muscle exhibits the greatest changes in structure of all the pelvic muscles among the three genera. In *Coccyzus* the tendinous middle portion of this muscle appears to hold the femur in a fixed plane with relation to the frontal plane. The progressive replacement by fleshy fibers of the central tendinous portion of its belly in *Crotophaga* and *Geococcyx* suggests the presence of control of the plane of movement of the femur with reference to the frontal plane, a necessity for balance on one foot in running. This trend seems also to be correlated with the progressive backward shift in the three genera of the fleshy fibers of the ilirotrochantericus posticus muscle. The anterior and posterior borders of the iliobtibialis muscle are fleshy and well developed in all three genera, though the increase in bulk and length of these fibers in *Crotophaga* and *Geococcyx* suggest a greater arc of thigh movement in the vertical plane.

The progressive migration craniolaterad in the three genera of the area of origin of the semitendinosus muscle and the consequently more nearly vertical action of its fibers with reference to both the sagittal and the transverse planes reduces its tendency to produce roll, lateral swing and vertical pitch in the axis as the trunk is propelled forward on the acetabular fulcrum. The progressive increase from *Coccyzus* to *Geococcyx* in bulk of this muscle indicates its importance in retraction of the thigh in the cursorial habit.

In speaking of the piriformis muscle, Hudson (1937: 21) pointed out that "There is a difference of opinion as to which end of the muscle constitutes the origin. Burt (1930: 502) considers the femoral attachment as the origin. Gadow based his interpretation of this question on the fact that the caudal attachment is on the vertebral column." Since both ends of pars caudofemoralis of the piriformis muscle are attached to movable bones, its contraction may draw either the femur caudad or the tail laterad and ventrad unless the tail is fixed by axial muscles. In the latter instance, both pars caudofemoralis and pars iliofemoralis would elevate the anterior portion of the axis, the head of the femur serving as a fulcrum. The far caudal point of origin of these muscles provides leverage for such action in bilateral or synchronous movement of the legs. Such a position of origin, however, would induce lateral movement of the axis in unilateral or alternate movement of the legs.

The absence of pars iliofemoralis in *Coccyzus*, the appearance of pars iliofemoralis and the reduction in strength of pars caudofemoralis in *Crotophaga*, and the further strengthening of the former and reduction of the latter in *Geococcyx* indicates the importance of vertical pull in eliminating swing and roll of the axis in alternate leg action.

The biceps femoris muscle is the strongest flexor of the crus. It is well developed in all three genera, which seems to indicate that flexion of the crus is equally important for the arboreal and the cursorial habit. Differences in it mainly are in extent of origin and degree of development of the belly. The point of insertion of the strong tendon of this muscle shows about the same relationship with respect to distance from the proximal end of the fibula in the three genera. The power arm in *Coccyzus*, therefore, may hold a slight advantage over that in *Crotophaga* and *Geococcyx* because of the greater absolute length of the tibiotarsus in the last two forms. This advantage in *Coccyzus*, however, appears to be offset by the progressive increase in bulk of the muscle in *Crotophaga* and *Geococcyx*.

The tibialis anticus muscle is the only muscle which flexes the tarso-metatarsus. This muscle is equally well developed in all three genera, but seems to exhibit in *Coccyzus* a mechanical advantage due to the relationship between the point of insertion of its tendon and the length of the tarsometatarsus.

The gastrocnemius muscle complex is responsible for extension of the tarsometatarsus. It is well developed in all three genera, but shows a progressive increase in length and bulk of its fleshy fibers from *Coccyzus* to *Geococcyx*. Associated with the greater development of the pars interna is a great enlargement of the inner cnemial crest in *Geococcyx* over that in the other two genera. The apparent strength of this muscle seems to be associated with a more complete extension of the tarsometatarsus in the propulsion for running in *Geococcyx* in contrast to the constantly flexed condition for perching in *Coccyzus*.

Stolpe (1932: 194) stated that the forward progression of the body of the bird is effected in part by movements occurring between the proximal phalanges and the trochleae of the tarsometatarsus. In addition to our interest in the muscles actuating the thigh, tibiotarsus and tarsometatarsus, therefore, we are interested in possible differences in the flexors and extensors of the digits.

The peroneus longus muscle aids in extending the tarsometatarsus and through its long tendon aids in flexing digit III. In *Coccyzus* this fusiform muscle is limited to the anterolateral aspect of the crus and is partially hidden by the tibialis anticus muscle. In *Crotophaga* and *Geococcyx*, however, its belly is greatly expanded and covers all other muscles on the anterior aspect of the crus including the tibialis anticus muscle. In these two genera, therefore, its development seems also to be correlated with a greater need for both extension of the tarsometatarsus and flexion of digit III.

The extensor digitorum longus muscle is the sole extensor of digits II, III and IV. From *Coccyzus* to *Geococcyx* the diameter of this muscle appears progressively to yield to length. This suggests an increase in extension of the

toes, an adaptation for spreading the foot on a flat surface rather than for grasping a limb.

Inasmuch as the direction of digit IV is reversed in the zygodactyl foot of the Cuculidae one would expect to find a trend in development of the extensor hallucis longus muscle similar to that found in the extensor digitorum longus. Such is not the case, however. The relative length of this muscle is greater in *Crotophaga* than in *Coccyzus* and *Geococcyx*, in which two genera it is about equal.

The development of the flexores perforati digiti II, III and IV is surprisingly uniform among the three genera. The flexores perforantes et perforati digiti II and III, however, show a difference in development the significance of which is not immediately clear. The belly of the flexor perforans et perforatus digiti II increases in length from *Coccyzus* to *Geococcyx*. This shift from a short, bulging head to a more slender belly appears to be correlated with both the loss of grasping power and increase in extensibility and flexibility of the digits in *Geococcyx* over *Coccyzus*. The flexor perforans et perforatus digiti III, on the other hand, is uniformly developed in the three genera. The explanation seems to lie in the much greater development of the peroneus longus muscle in *Geococcyx* and *Crotophaga* than in *Coccyzus*. The long tendon of this muscle inserts on the tendon of the flexor perforatus digiti III muscle and thus augments the flexing action of that muscle on digit III.

The major flexors of the digits—flexor digitorum longus and flexor hallucis longus—appear to be of little aid in explaining the change from synchronous to alternate leg action. The flexor digitorum longus muscle seems to be uniformly developed in the three genera. The belly of the flexor hallucis longus muscle shows a progressive increase in length from *Coccyzus* to *Geococcyx*. One would expect that greater flexion of the hallux would be more important for grasping a branch than for running. The vinculum connecting the tendons of these two muscles varies in its form among the three genera but the differences are probably not functionally important.

The development of the short toe muscles varies among the three genera and, likewise, does not follow a definite pattern. Steinbacher (1935: 251-255, 277) called attention to the fact that no given type of foot is adapted for only one particular use and cited the zygodactyl Cuculidae as an example. Extensor proprius digiti III shows a progressive decrease in length but an increase in bulk of the fleshy fibers from *Coccyzus* to *Geococcyx*. The greater bulk in *Geococcyx* seems to indicate that strong extension of the proximal phalanx of digit III is important in terrestrial locomotion. A progressive reduction in length of belly of the flexor hallucis brevis relative to length of tarsometatarsus would indicate less capacity for flexion of the proximal phalanx of the hallux in *Geococcyx* as compared to *Coccyzus*. Abductor digiti II is progressively weaker from *Coccyzus* to *Geococcyx* suggesting that abduction of digit II is more important for perching than for running. Differences between the extensor brevis digiti IV and the adductor digiti II muscles among the three genera are believed to be functionally not significant.

A comparison of the data presented above indicates certain major adapta-

tions in the pelvic appendage of the cursorial road-runner from its assumed cuckoo-like ancestor. The tendency to produce roll and lateral swing of the body axis under alternate leg action in *Geococcyx* is reduced by a shift laterad towards the vertical in direction of pull of two of the retractor muscles of the thigh. This shift is effected partly by the craniolateral migration of the origin of the semitendinosus muscle and partly by an increase in development of the pars iliofemoralis simultaneously with a decrease in development of the pars caudofemoralis of the piriformis muscle. The tendency to produce roll of the body axis in *Geococcyx* is further reduced by: (1) the increased development of pars iliofemoralis (with a lateral point of origin) and the reduction in strength of pars caudofemoralis (with a mesial origin) of the piriformis muscle; (2) the caudal migration of the origin of the iliotrochantericus posticus muscle; and (3) the replacement by fleshy fibers of the central tendinous portion of the belly of the iliotibialis muscle.

Differences in development of the several flexors and extensors of the digits are difficult to interpret because they do not seem to follow a clear cut pattern. In general it would appear that in the road-runner there is a need for greater extension of the tarsometatarsus and a greater range of extensibility and flexibility of the digits. This greater range could be gained by an increase in the length of the bellies of the several muscles. Conversely, it appears that full extensibility and strength at partial flexion in the road-runner would be replaced by power at full flexion of the digits for perching in the arboreal cuckoos.

The fact that the differences in some muscles follow the pattern suggested above and that other muscles appear not to follow this pattern may be interpreted in two ways: (1) the author may have failed to detect differences or trends of development in certain muscles; (2) there are definite limitations to interpretation of functional differences in gross anatomical studies. The relationship between the amount of aponeurosis and tendon to the fleshy fibers of a muscle has a direct bearing on the amount and kind of work which that muscle can perform, but there is no known method for determining this relationship. At the present time, I have been able to obtain only a translator's abstract of a recent paper by Nel (1940) in which he described two types of muscle fibers in leg muscles of birds. The quantitative distribution of these two fiber types was found to be correlated with the mode of locomotion of the birds studied. It seems likely, therefore, that similarity in the external form among the three genera of some of the pelvic muscles does not preclude histological differences which could account for differences in the function of these muscles.

Inasmuch as cursorial animals tend to possess longer appendages than do arboreal animals, an increase in length of the skeletal elements of the leg must be advantageous in terrestrial locomotion. The relative increase in development of certain protractor and retractor muscles of the thigh in *Geococcyx* over *Coccyzus* must also facilitate the rapid alternate leg action characteristic of the road-runner. The total myology of the leg in the three genera is so uniform, however, that I believe that the main factor contributing to the dif-

ference in locomotion in these birds is the increase in length of distal skeletal elements in *Geococcyx*.

I believe, also, that another factor must play considerable importance in this difference in locomotion: namely, the innate behavior pattern of these birds. The ani usually employs alternate leg action when on the ground and in nearly all anatomical characters considered it exhibits an intermediate stage of development between *Coccyzus* and *Geococcyx*. I have never seen a cuckoo (*Coccyzus*) use alternate leg action when on the ground, but the structure of the pelvic appendage leads me to believe that should its nervous pattern require it this bird would be able to do so, even though the relatively short legs would make such a method of locomotion awkward.

ON THE CLASSIFICATION OF THE CUCULIDAE

The family Cuculidae contains 38 genera and 127 species allocated to six subfamilies (Peters, 1940: 12-76; Mayr, 1946: 66). The attitude of contemporary ornithologists toward the classification of cuckoos is indicated by the following statement made (*in litt.*) by James L. Peters of Harvard University: "The cuckoos are a very involved family and for this reason the question of subfamilies has bothered ornithologists for years and the number of these groups has varied from ten to three. My classification was based on what I considered the best features [of earlier systems of classification]. . . . The subfamily Phacnicophaeinae is admittedly more of a general 'catchall' for genera that cannot be satisfactorily allocated in the other subfamilies." Garrod (1873: 633) proposed that the Cuculidae be divided into *two* subfamilies according to whether or not they possessed the *M. piriformis* pars iliofemoralis (equals *M. accessorius* femorocaudal).

In view of the confusion which exists regarding the relationship among the genera of this family, it would be well to consider some of the characters which have been utilized in the several systems of classification proposed. Garrod (1873, 1874) proposed that certain muscles of the thigh of birds could be used to advantage in classification. He designated these muscles by assigning a letter to each. Consequently, a simple muscle formula would indicate which of these muscles were present or absent in any species or larger category. The muscles used and their letter designations are: *M. piriformis* pars caudofemoralis, A; *M. piriformis* pars iliofemoralis, B; *M. semitendinosus*, X; *M. accessorius* semitendinosi, Y. In addition, the presence or absence of *M. ambiens* was indicated in the formulae by a plus or minus sign respectively. In 1875 Garrod emphasized the importance in classification of the form assumed by the vinculum connecting the tendons of *M. flexor digitorum longus* and *M. flexor hallucis longus*. The value in classification of such a myological formula immediately was perceived by ornithologists. As a result, all authors presenting a thorough treatment of the subject have included in their technical diagnosis of the families and orders of birds the myological formulae of Garrod (as supplemented especially by Beddard, Forbes and Gadow). For a period of nearly forty years little work was done in avian anatomy. The studies of Burt (1930) and Hudson (1937) revived interest

in this field. The results of the thorough investigation of Hudson led him to propose a modification of Garrod's formulae because he discovered that certain other muscles of the leg were more variable throughout the orders of birds than were some of those used by Garrod. Hudson proposed that the following muscles be added to the formulae: *M. iliotrochantericus medius*, C; *M. gluteus medius et minimus*, D. He proposed that *M. ambiens* be designated by the symbol "Am," and pointed out that the vinculum between the tendons of *M. flexor digitorum longus* and *M. flexor hallucis longus* was of little importance because it is present in all groups of birds except the *Passeriformes* and *Upupa*. He further proposed, therefore, that the more variable vinculum connecting the tendons of *M. flexor perforatus digiti III* and *M. flexor perforans et perforatus digiti III* be added to the formula and designated by the letter V.

In 1877 Garrod presented his results on investigations of the syrinx and its importance in classification. This paper pertained to the classification of the *Passeriformes*, but Beddard (1885, 1901) used the structure of the syrinx in the classification of cuckoos. Beddard (*ibid.*) introduced the condition of the "ventral feather tract" as an aid in establishing subfamilies. Shelley (1891), in determining the subfamilies of *Cuculidae*, employed number of rectrices, length of the upper tail coverts, length and shape of the wing, relationship of primaries to secondaries, and shape of the claw of the hallux. Knowlton (1909: 446) used the shape of the nares, round or oval, as a taxonomic character in the cuckoos, and Sharpe (1873) used the feathering of the tarsi and the condition of nares (swollen or not swollen) in classifying the *Cuculidae* of the Ethiopian Region.

The anatomical characters listed above represent the main ones which have been used in the classification of the cuckoos. No one author has used all of these characters and data on these characters for all genera are not available in the literature. Before a satisfactory division of the *Cuculidae* can be made it will be necessary to examine each genus in the family with respect not only to all of these characters but to other anatomical features as well.

Until about twenty years ago only anatomical features were used in systems of classification of the cuckoos. The modern trend in systematics, however, is to consider behavior, ecology and geographical distribution as well as anatomy in determining the degree of relationship among genera. Baker (1927) partially distinguished the *Cuculinae* from the *Phaenicopterinae* by stating that the former are parasitic while the latter are non-parasitic. Bannerman (1938) and Delacour (1947) also made use of this character. Baker (1927), Delacour (1947) and Delacour and Mayr (1946) referred to the habits of some of the subfamilies, i.e., "terrestrial"; "Large, long-legged cuckoos that live and feed on the ground, although they roost at night and nest in trees"; "Habitat is tall trees." Delacour (1947) and Delacour and Mayr (1946) referred to limitations in distribution of certain subfamilies (e.g., "The true cuckoos are an entirely Old World group") although it is not clear how much importance these authors attached to this factor. The importance of para-

sitism in ascertaining genetic relationship has been established by Friedmann (1928, 1929, 1948).

The present writer feels that a satisfactory reclassification can be accomplished only after each genus has been studied both anatomically and ecologically. The old criteria must be examined comparatively in the various genera and new criteria must be sought. The crux of the problem lies in determining just what constitutes adequate criteria for subdividing on the subfamily level. There can be little doubt that different authorities would disagree on the answer to this question. It seems inevitable, however, that morphological criteria must be considered. Hudson (1937: 62) has pointed out that "Myological characters are of taxonomic value only when they are employed with due regard to all other known morphological facts." Nevertheless, within the limits of a given family, the myological formulae certainly must be of greater significance than are external characters which are readily subject to adaptive changes: i.e., size and shape of bill and the length and shape of the claw of the hallux.

It seems evident that certain elements of the skeleton, also, reveal basic relationships. It has been shown, and is generally accepted, that the vertebral column is less subject to change during the evolutionary process than are the appendages. The components of the several regions of the axial skeleton, therefore, appear to be valuable aids in determining relationship among larger groups. There is a positive correlation between the relative length of the elements composing the pectoral and pelvic appendages and the locomotor habits of the birds. Their more responsive features, therefore, should be useful in determining relationships within the larger groups.

An analysis of data obtained in this study leads me to suggest that the following anatomical characters may reveal systematic differences if studied in all genera of the Cuculidae.

Axial skeleton.—As pointed out above (p. 517) there is disagreement in literature on the number of cervical vertebrae present in the Cuculidae. Most writers state that the family is characterized by possessing 14 cervical vertebrae. Fürbringer (1888: 778-779) gave 13 as the number in *Crotophaga*. Shufeldt (1901: 42), however, stated that the members of the Crotophaginae possess 14 cervical vertebrae. My data indicate that there are 14 in *Crotophaga sulcirostris*. I have been able to count only 13 cervical vertebrae in *Coccyzus a. americanus*, *C. a. occidentalis* and *C. erythrophthalmus*. Although the number of dorsal vertebrae was found to be constant in the genera examined, this region of the axial skeleton should be investigated. An embryological study of the formation of the synsacrum and the pygostyle should yield pertinent information.

Disc of pygostyle.—Comparative studies of the pygostyle would undoubtedly cast more light on the functional significance of the disc.

Wing-leg proportions.—Biometric analyses of each genus (such as has been done here) would enable one to construct a complete osteological series showing the strictly arboreal forms (i.e., primitive—Beebe, 1915; Engels, 1938: 207; Gregory, 1916: 37-38; Heilmann, 1927: 201-202), the strictly terrestrial

forms (i.e., most specialized—Larson, 1930: 424) and varying degrees of intermediacy between these extremes. These data would aid materially in establishing relationships.

Myology.—The detailed myological features of the wing and also the following points in the myology of the leg should be determined: (a) The presence or absence of *M. piriformis* pars iliofemoralis; (b) The presence or absence of the vinculum connecting the tendons of *M. flexor perforatus digiti III* and *M. flexor perforans et perforatus digiti III*; (c) The relationship of the proximal extent of the origin of *M. femorotibialis internus* to the insertion of *M. iliacus*; (d) The presence or absence of an accessory insertion of *M. semimembranosus* on *M. gastrocnemius*. This accessory insertion is present in *Crotophaga* and *Geococcyx* (see p. 538); (e) The presence or absence of a connection between the tendon of *M. semitendinosus* and *M. semimembranosus* (see Hudson, 1937: 23). Such a connection is wanting in the three genera reported on in this paper; (f) The presence of one or two heads of *M. obturator externus*; (g) Whether or not the tendon of *M. flexor perforans et perforatus digiti II* is perforated by the tendon of *M. flexor digitorum longus* (see pp. 550-551); (h) The shape of *M. obturator internus*. Garrod (1881: 325) discussed "The area of Origin of the Obturator Internus." Shufeldt (1886b: 478) in speaking of *Geococcyx* said: "Prof. Garrod laid some stress on the point whether this muscle arose from a triangular or an oval area. Here it arises from a decidedly oval one. . . ." Shufeldt misinterpreted Garrod's point since the latter author said: "In a large number of birds, on looking at the pelvic view of this muscle when undisturbed, its shape is seen to be an elongated oval. . . . In another large number of birds, instead of being oval it is triangular." Furthermore, Garrod (p. 329) presented a table summarizing the shape of this muscle in certain families of birds and stated that this muscle is triangular in the Cuculidae. Garrod did not state how many genera he examined, but data he presented in other papers indicate that it was not a large number. In the three genera which I have examined, however, this muscle, when viewed in the *undisturbed condition*, is distinctly triangular in shape.

SUMMARY

Data presented here reveal a greater degree of individual variation in certain skeletal elements than literature on birds in general indicates. This is especially true of the number of fused vertebrae in the synsacrum and the number of free caudal vertebrae, the former varying from 11 to 13 and the latter from 4 to 6.

Geococcyx californianus and *Crotophaga sulcirostris* possess 14 cervical vertebrae each, whereas two species of *Coccyzus* possess only 13 cervical vertebrae each. The cervical region seems to show little or no variation, in contrast with the more caudal portions of the vertebral column.

Members of the three genera possess 4 dorsal vertebrae each.

The length of the cranium is less variable than either the length of the synsacrum or the length of the dorsal vertebral region.

The development of the disc on the pygostyle in *Coccyzus* is correlated with the high degree of development of pars caudofemoralis of the piriformis muscle in that genus. In *Crotophaga* and *Geococcyx*, where pars caudofemoralis exhibits a progressive reduction in development, such a disc is absent.

Ratios between the depth of the carina and the total length of the sternum reflect differences in flying ability among the three genera. This is especially noticeable in the cursorial road-runner.

There is an increase in the absolute length of both the wing and the leg as we pass from *Coccyzus* to *Geococcyx*, and there is a relative increase in the length of the several segments of the pelvic appendage in the same series. Conversely, excepting the humerus of *Geococcyx*, there is a relative decrease in the length of each segment of the pectoral appendage in both *Crotophaga* and *Geococcyx* from that in *Coccyzus*. There is a progressive increase in the length of the several leg segments and a progressive decrease in the length of the several wing segments distally in *Geococcyx* in relation to *Coccyzus*, whereas the limb segments of *Crotophaga* do not follow this pattern, except possibly in the leg.

The muscle formula of the genus *Coccyzus* is AXYAm. Of the forty-three pelvic muscles described for birds, the following are absent in this genus: M. iliотrochantericus medius; M. gluteus medius et minimus; M. piriformis pars iliofemoralis; M. adductor digiti IV; M. extensor brevis digiti III (described only for Ratites—see Hudson, 1937: 54). A vinculum connecting the tendons of M. flexor digitorum longus and M. flexor hallucis longus is present, but a vinculum is wanting between the tendons of the flexor perforatus digiti III and the flexor perforans et perforatus digiti III muscles. The tendon of M. flexor perforans et perforatus digiti II does not ensheath the tendon of M. flexor digitorum longus supplying digit II.

The muscle formula of *Crotophaga sulcirostris* and *Geococcyx californianus* is ABXYAm. These genera lack the same muscles as does *Coccyzus*, except that pars iliofemoralis of the piriformis muscle is present in these genera.

Shufeldt overlooked the following muscles in his description of the pelvic musculature of *Geococcyx*: M. iliacus, M. adductor digiti II, and M. lumbricalis. In addition, he grouped M. extensor hallucis longus, M. abductor digiti II, M. extensor proprius digiti III, and M. extensor brevis digiti IV under the description of one muscle—namely, M. extensor brevis digitorum. Although he described M. gastrocnemius pars media, the description he gave is for the medial head of pars externa of the gastrocnemius muscle.

I was unable to demonstrate in either *C. a. americanus* or *C. erythrophthalmus* the accessory tendon of insertion of M. tibialis anticus (see Hudson, 1937: 30, 72).

A review of the locomotor habits of the three genera is given.

Because of bilateral action of muscles of the leg, a hopping bird is able to maintain passive balance of the axis in the transverse plane (to prevent horizontal roll) and in the frontal plane (to prevent lateral swing), but not in the midsagittal plane. Failure to maintain balance in the midsagittal plane

results in a tendency for the axis alternately to pitch upward and downward during retraction of the leg. Unilateral action of muscles in a running bird necessitates dynamic balance in all three planes in order to minimize pitch, roll and swing of the axis.

The direction of pull of a muscle in relation to these three planes of the axis determines the amount of pitch, roll and swing which result from contraction of the muscle in unilateral leg action. The pull of most muscles is not limited to one plane, but the resultant action of such a muscle may be resolved into its component parts. The caudal pull of a muscle arising from a median axial structure caudal to its point of insertion results in dorsoventral pitch of the axis. The dorsomesial pull of a muscle arising dorsal and mesial to its point of insertion results in horizontal roll of the axis toward the side of contraction. The caudomesial pull of a muscle arising caudal and mesial to its point of insertion results in lateral swing of the axis. The progressive cranial and lateral shift of the origin of several pelvic muscles from *Coccyzus* to *Geococcyx* increases the vertical pull of these muscles and, thereby, decreases the tendency for pitch, roll, and swing of the axis. This shift is effected partly by the craniolateral migration of the origin of the semitendinosus muscle and partly by an increase in development of the pars iliofemoralis simultaneously with a decrease in development of the pars caudofemoralis of the piriformis muscle. The tendency to produce roll of the body axis in *Geococcyx* is further reduced by (1) the increased development of pars iliofemoralis and the reduction in strength of pars caudofemoralis of the piriformis muscle; (2) the caudal migration of the origin of the iliotochantericus posticus muscle; and (3) the replacement by fleshy fibers of the central tendinous portion of the belly of the iliotibialis muscle.

Differences in the development of the several flexors and extensors of the digits do not seem to follow a clear cut pattern. In general, it appears that in the cursorial road-runner, there is need for greater extension of the tarsometatarsus and a greater range of extensibility and flexibility of the digits, the latter being an adaptation for spreading the toes on a flat surface. Adaptation for this greater range of extension and flexion are to be found in the increased length and bulk of the gastrocnemius, peroneus longus, extensor digitorum longus, and flexor hallucis longus muscles in *Geococcyx* over *Coccyzus*. Concomitant adaptations, however, are not found in the development of the flexor digitorum longus or extensor hallucis longus muscles.

It seems likely that histological differences in some of the pelvic muscles may account for differences in function even though the external form of the muscles may be similar in the three genera. Such differences in structure could account either for full extensibility and strength at partial flexion or for greatest strength at full flexion of the digits.

It is suggested by the writer that the differences in habits exhibited by the three genera may be explained most satisfactorily by reference to the increased leg length in *Geococcyx*. The increase in relative development and changes in proportion of certain leg muscles in this bird facilitates but is not responsible for terrestrial locomotion and alternate leg action. It is further suggested that

the innate behavior pattern plays an important role in determining the locomotor pattern distinctive of the three genera.

Difficulties involved in the classification of the Cuculidae are discussed. A satisfactory reclassification of this family will not be feasible until each genus is studied anatomically and ecologically. The osteological and myological characters which should be investigated in each genus are listed. On the basis of number of rectrices, limb proportions, muscle formula (ABXYAm) and general habits the genera *Crotophaga* and *Geococcyx* should be maintained in separate subfamilies as at present. On the basis of the muscle formula of the leg (AXYAm), the genus *Coccyzus* cannot be included in the subfamily Phaenicopterinae (ABXYAm) as given by Peters (1940: 41). On the basis of the number of cervical vertebrae, this genus does not fit into any of the six subfamilies currently proposed. In view of the stability of the cervical region of the vertebral column, this difference in the number of cervical vertebrae seems sufficient to warrant placing the genus *Coccyzus* in a separate subfamily.

REFERENCES

- ADAMS, L. A. 1938—An introduction to the vertebrates. 2nd Ed. 479 pp. John Wiley & Sons, Inc., New York.
- BAKER, E. C. S. 1927—The fauna of British India, including Ceylon and Burma. Birds, vol. IV, 2nd Ed., Taylor and Francis, London, 471 pp., 71 figs. in text, 7 col. plates.
- BANNERMAN, D. A. 1933—The birds of tropical West Africa, with special reference to those of the Gambia, Sierra Leone, the Gold Coast and Nigeria. vol. III, Crown Agents for the Colonies, London, 487 pp., 144 figs., 12 col. plates, 1 map.
- BEDDARD, F. E. 1885—On the structural characters and classification of the cuckoos. Proc. Zool. Soc. London: 168-187, 7 figs.
- 1898a—On the anatomy of an Australian Cuckoo, *Scythrops novae-hollandiae*. Ibid. 44-49, 4 figs.
- 1898b—The structure and classification of birds. Longmans, Green, and Co., London, xx+548 pp.
- 1901—On the anatomy of the Radiated Fruit Cuckoo (*Carpococcyx radiatus*). Ibis 1, Eighth Series: 200-214.
- BENT, A. C. 1940—Life histories of North American Cuckoos, Goatsuckers, Hummingbirds and their allies. U.S.N.M. Bull. No. 176, 506 pp., 73 pls.
- BEEBE, C. W. 1915—A tetrapteryx stage in the ancestry of birds. Zoologica 2(2): 39-52, figs. 7-11.
- , G. INNESS HARTLEY, AND PAUL G. HOWES 1917—Tropical wild life in British Guiana. I, New York Zool. Soc. 504 pp.
- BOAS, J. E. V. 1933—Kreuzbein, Becken und Plexus lumbosacralis der Vögel. Det Kongelige Danske Videnskabernes Selskabs Skrifter. Naturvidenskabelig og Matematisk Afdeling 9 række, 1: 5-74, 33 text-figs., 15 pls.
- BÖKER, HANS 1927—Die biologische Anatomie der Flugarten der Vögel und ihre Phylogenie. Jour. für Ornithologie 75: 304-371, 20 tables, 112 text-figs.
- 1935—Einführung in die Vergleichende Biologische Anatomie der Wirbeltiere. Erster Band, 228 pp., mit 225 abbildungen im Text., Gustave Fischer, Jena.
- BURT, W. H. 1930—Adaptive modifications in the woodpeckers. Univ. Calif. Pub. Zool. 32(8): 455-524.
- CHAMBERLAIN, F. W. 1943—Atlas of avian anatomy, osteology, arthrology, and myology. Mich. Agric. Experiment Station Mem. Bull. 5, 47 pp., 95 pls.
- COTTAM, C., C. S. WILLIAMS AND C. A. SOOTER 1942—Flight and running speeds of birds. Wilson Bull. 54: 121-131.

- COUES, ELLIOTT 1866—The osteology of the *Columbus torquatus*; with notes on its myology. Mem. Boston Soc. Nat. Hist. 1, pt. 2: 131-172, 2 figs., 1 pl.
- 1903—Key to North American birds. 5th ed., 2 vols., Dana Estes and Co., Boston.
- DAVIS, D. E. 1940—Social nesting habits of the Smooth-billed Ani. Auk 57(2): 179-218.
- DELACOUR, J. 1947—Birds of Malaysia. Macmillan Co., New York, 382 pp., 84 figs.
- AND ERNST MAYR 1945—Birds of the Philippines. Ibid. 309 pp., 69 figs.
- EATON, E. H. 1914—Birds of New York. Part 2, Mem. 12, New York State Museum, Albany, 7:9 pp., 106 pl.
- ENGELS, W. L. 1938—Cursorial adaptations in birds. Limb proportions in the skeleton of Geococcyx. Jour. Morph. 63(2): 207-217.
- 1940—Structural adaptations in thrashers (Mimidae: Genus *Toxostoma*) with comments on interspecific relationships. Univ. Calif. Pub. Zool. 42(7): 341-400.
- FISHER, H. I. 1946—Adaptations and comparative anatomy of the locomotor apparatus of New World vultures. Amer. Midl. Nat. 35(3): 545-727, figs. 28, pls. 13.
- FORBUSH, E. H. 1929—Birds of Massachusetts and other New England States. vol. II, Mass. Dept. Agric., Norwood, Mass., 461 pp., 62 pls.
- FRIEDMANN, H. 1928—The Origin of host specificity in the parasitic habit in the Cuculidae. Auk 45(1): 33-38.
- 1929—The Cowbirds. A study in the biology of social parasitism. Charles C. Thomas, Springfield, 421 pp.
- 1948—The parasitic cuckoos of Africa. Monograph no. 1, Wash. Acad. Sci., Washington, 204 pp.
- FÜRBRINGER, MAXIMILIAN 1888—Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane. 2 vols., 1751 pp., 30 taf., Jena.
- GADOW, HANS 1892—On the classification of birds. Proc. Zool. Soc. London: 229-256.
- 1933—The evolution of the vertebral column. A contribution to the study of vertebrate phylogeny. Univ. Press, Cambridge, xiv+356 pp.
- UND EMIL SELENKA 1891-1893—Bronn's Klassen und Ordnungen des Tier-Reichs, in Wort und Bild. 2 vols., Anatomischer Theil, 1891, 1008 pp. Systematischer Theil, 1893, 303 pp.
- GARROD, A. H. 1873—On certain muscles of the thigh of birds and on their value in classification. Part I. Proc. Zool. Soc. London: 626-644, 6 figs.
- 1874—On certain muscles of birds and their value in classification. Part II. Ibid. 111-123, 1 pl.
- 1875—On the disposition of the deep plantar tendons in different birds. Ibid. 339-348, 9 figs.
- 1877—On some anatomical peculiarities which bear upon the major divisions of the passerine birds. Part I. Ibid. 506-519, pls. 48-53.
- 1881—The collected scientific papers of the late Alfred Henry Garrod. W. A. Forbes, ed., London, xxv+537 pp.
- GEGENBAUR, CARL 1878—Elements of comparative anatomy. Macmillan and Co., London, xxvi+645 pp.
- GREGORY, W. K. 1916—Theories of the origin of birds. Ann. New York Acad. Sci. 27: 31-38.
- HEILMAN, G. 1926—The origin of birds. H. F. & G. Witherby, London, 208 pp., 140 figs., 2 pls.
- HOWELL, A. B. 1926—Anatomy of the wood rat. Monog. Am. Soc. of Mammalogists, no. 1, Williams and Wilkins Co., Baltimore, 225 pp., 36 figs. in text.
- 1938—Muscles of the avian hip and thigh. Auk 55(1): 71-81, 2 figs.
- HOWARD, H. 1929—The avifauna of Emeryville Shellmound. Univ. Calif. Pub. Zool. 32(2): 301-394.
- HUDSON, G. E. 1937—Studies on the muscles of the pelvic appendage in birds. Amer. Midl. Nat. 18(1): 1-108.
- 1948—Studies on the muscles of the pelvic appendage of birds II: The hetero-

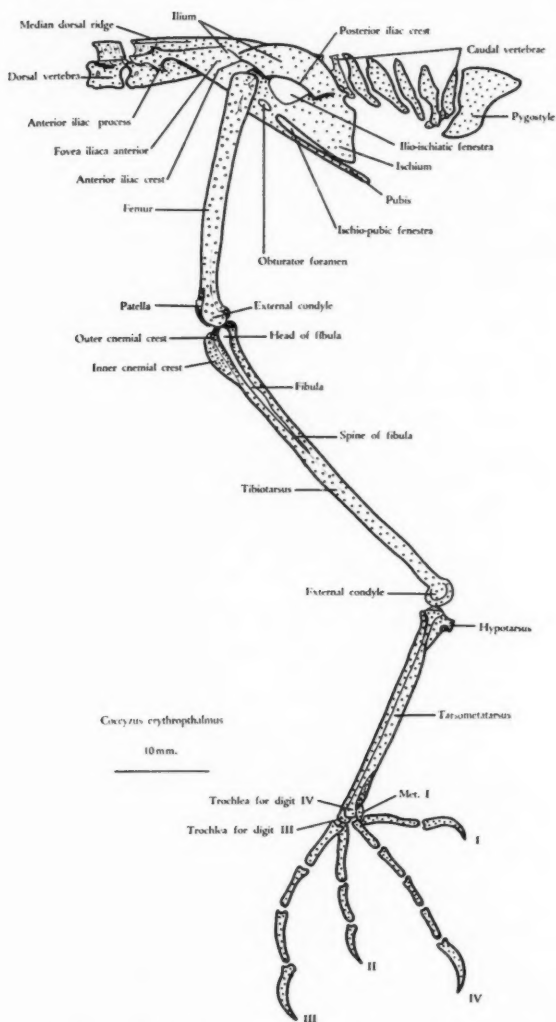
- geneous order Falconiformes. *Ibid.* 39(1): 102-127.
- HUXLEY, T. H. 1867 On the classification of birds; and on the taxonomic value of the modifications of certain of the cranial bones observable in that class. *Proc. Zool. Soc. London*: 415-472.
- 1868—On the classification and distribution of the Alectoromorphae and Heteromorphae. *Ibid.* 294-319.
- 1872—A manual of the anatomy of vertebrated animals. D. Appleton and Co., New York, 431 pp.
- KNOWLTON, F. H. 1909—Birds of the world. Henry Holt Co., New York, 873 pp., 233 figs., colored frontis.
- LARSON, L. M. 1930—Osteology of the California Road-runner: Recent and Pleistocene. *Univ. Calif. Pub. Zool.* 32(4): 409-428.
- LUCAS, F. A. 1888—Abnormalities in the ribs of birds. *Auk* 5(3): 329-330.
- 1889—Costal variations in birds. *Ibid.* 6(2): 195-196.
- 1893—Individual skeletal variation. *Science* 22(547): 52-53.
- MARPLES, B. J. 1930—The proportions of birds' wings and their changes during development. *Proc. Zool. Soc. London*: 997-1008, 7 figs.
- MARSH, O. C. 1880—Odontornithes: a monograph on the extinct toothed birds of North America. U. S. Geological Exploration of the Fortieth Parallel. Government Printing Office, Washington, D. C., xv+201 pp.
- MAYR, E. 1946—The number of species of birds. *Auk* 63(1): 64-69.
- MILLER, A. H. 1937—Structural modifications in the Hawaiian Goose (*Nesochen sandvicensis*). A study in adaptive evolution. *Univ. Calif. Pub. Zool.* 42(1): 1-80, plates 1-6, 12 figs. in text.
- MIVART, ST. G. 1879—On the axial skeleton of the Pelecanidae. *Trans. Zool. Soc. London*: 10: 315-378.
- NEL, J. TH. 1940—Histologische und anatomische Untersuchungen an der Hinterextremität einiger Vögel. *Verhandl. naturhist. ned. Ver. Heidelberg* 18(3): 223-244.
- NEWTON, A. 1896—A dictionary of birds. Adam and Charles Black, London, xii+1088 pp.
- OWEN, R. 1866—On the anatomy of vertebrates. Longmans, Green and Co., London, vol. II, Birds and Mammals, viii+592 pp.
- 1879—Memoirs on the extinct wingless birds of New Zealand: with an appendix on those of England, Australia, Newfoundland, Mauritius, and Rodriguez. John Van Voorst, London I: x+465.
- PARKER, R. J. AND W. A. HASWELL 1947—A text book of zoology. Macmillan and Co. Ltd., London, 6th ed., vol. II, xxviii+758 pp.
- PARKER, W. K. 1876—On the structure and development of the birds' skull. Part II. *Trans. Linnean Soc. London, 2nd Series, vol. I, Zoology.* pp. 99-154.
- PETERS, J. L. 1940—Check-list of birds of the world. Harvard Univ. Press, Cambridge, vol. IV, 291 pp.
- PYCRAFT, W. P. 1903—Contributions to the osteology of birds. Part VI. Cuculiformes. *Proc. Zool. Soc. London*: 258-291.
- RICHARDSON, F. 1942—Adaptive modifications for tree-trunk foraging in birds. *Univ. Calif. Pub. Zool.* 46(4): 317-368.
- ROMER, A. S. 1945—Vertebrate paleontology. 2nd ed. Univ. Chicago Press, Chicago, 687 pp., 377 figs., 4 pls.
- SHARPE, R. B. 1873—On the Cuculidae of the Ethiopian Region. *Proc. Zool. Soc. London*: 578-624.
- SHELLEY, G. E. 1891—Catalogue of the Picariae in the collection of the British Museum. Taylor and Francis, London, 484 pp., 13 col. plates.
- SHUFELDT, R. W. 1881—Osteology of *Speotyto cunicularis hypogaea*. 12th annual report of the U. S. Geol. and Geog. Survey of the Territories for the year 1878, Part I by F. W. Hayden, pp. 593-626.
- 1882—Osteology of the North American Tetraonidae. *Ibid.* 653-718.
- 1884—Osteology of *Ceryle alcyon*. *Jour. Anat. & Phys., London*, 18, pt. 3: 279-294.

- 1886a—The skeleton in *Geococcyx*. *Ibid.* 20: 244-266.
 —1886b—Contributions to the anatomy of *Geococcyx californianus*. *Proc. Zool. Soc. London*: 466-491, pls. xlii-xlv.
 —1888—On the affinities of *Aphriza virgata*. *Jour. Morph.* 2(2): 311-340, pl. 25.
 —1890—The myology of the Raven (*Corvus corax sinuatus*). Macmillan and Co., London, 343 pp., 76 figs.
 —1901—The osteology of the Cuckoos. *Proc. Amer. Phil. Soc.*, Philadelphia, 40(165): 4-51.
 —1909—Osteology of birds. New York State Museum Bull. No. 130, Albany, 381 pp.
 STEINBACHER, G. 1935—Funktionell-anatomische Untersuchungen an Vogelfüssen mit Wendzehen und Ruckzehen. *Jour. für Ornithologie* 83: 214-282, 33 figs. in text.
 STOLPE, M. 1932—Physiologisch-anatomische Untersuchungen über die hintere Extremität der Vögel. *Ibid.* 80(2): 161-247, 47 figs. in text.
 STORER, R. W. 1945—Structural modifications in the hind limb in the Alcidae. *Ibis* 87: 433-456, text figs. 7-13.
 WIEDERSHEIM, R. 1909—Vergleichende Anatomie der Wirbeltiere. Gustav Fischer, Jena, xx+935 pp.
 WILCOX, H. H. 1948—The pelvic musculature of the Loon, *Gavia immer*. 95 pp., 26 pls. (Microfilm thesis, Univ. Mich.)
 ZITTEL, K. A. 1932—Text-book of paleontology. Macmillan and Co., Ltd., London, vol. II: xvii+464 pp.

LIST OF ABBREVIATIONS USED IN PLATES

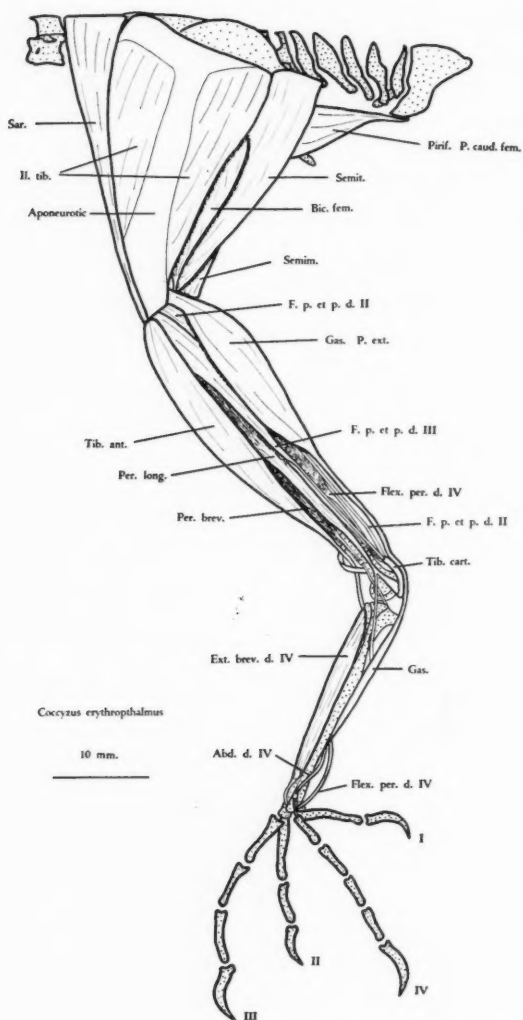
- | | |
|---|---|
| Abd. dig. II—M. abductor digiti II | Flex. per. d. IV—M. flexor perforatus digiti IV |
| Abd. d. IV—M. abductor digiti IV | Gas.—M. gastrocnemius |
| Acc.—M. accersoris semitendinosi | Iliac's—M. iliacus |
| Add. d. II—M. adductor digiti II | Il. tib.—M. iliobibialis |
| Add. long.—M. adductor longus et brevis | Il. troc. ant.—M. ilioprochanticus anticus |
| Ambiens—M. ambiens | Il. troc. post.—M. ilioprochantericus posticus |
| Auto. ext.—Automatic extensor | Isch. fem.—M. ischiofemoralis |
| Auto. flex.—Automatic flexor | Lumb.—M. lumbrical s |
| Bic. fem.—M. biceps femoris | Met. I—Os metatarsal I |
| Bic. loop—Biceps loop | Mm. il. troc.—Mm. ilioprochanterici |
| Ext. brev. d. IV—M. extensor brevis digiti IV | Obt. ext.—M. obturator externus |
| Ext. dig. I.—M. extensor digitorum longus | Obt. int.—M. obturator internus |
| Ext. hal. I.—M. extensor hallucis longus | P. caud. fem.—Pars caudofemoralis |
| Ext. pro. d. III—M. extensor proprius digiti III | P. ext.—Pars externa |
| Fem. tib.—M. femorotibialis | P. il. fem.—Pars iliofemoralis |
| Fem. tib. ext.—M. femorotibialis externus | P. int.—Pars interna |
| Fem. tib. int.—M. femorotibialis internus | P. med.—Pars media |
| Fem. tib. med.—M. femorotibialis medius | Pat. ten.—Patellar tendon |
| F. dig. I.—M. flexor digitorum longus | Per. brev.—M. peroneus brevis |
| F. hal. brev.—M. flexor hallucis brevis | Per. long.—M. peroneus longus |
| F. hal. l.—M. flexor hallucis longus | Pirif.—M. piriformis |
| F. p. et p. d. II—M. flexor perforans et perforatus digiti II | Plan.—M. plantaris |
| F. p. et p. d. III—M. flexor perforans et perforatus digiti III | Pop.—M. popliteus |
| Flex. per. d. II—M. flexor perforatus digiti II | Sar.—M. sartorius |
| Flex. per. d. III—M. flexor perforatus digiti III | Semim.—M. semimembranosus |
| | Semit.—M. semitendinosus |
| | Tib. ant.—M. tibialis anticus |
| | Tib. cart.—Tibial cartilage |

PLATE I



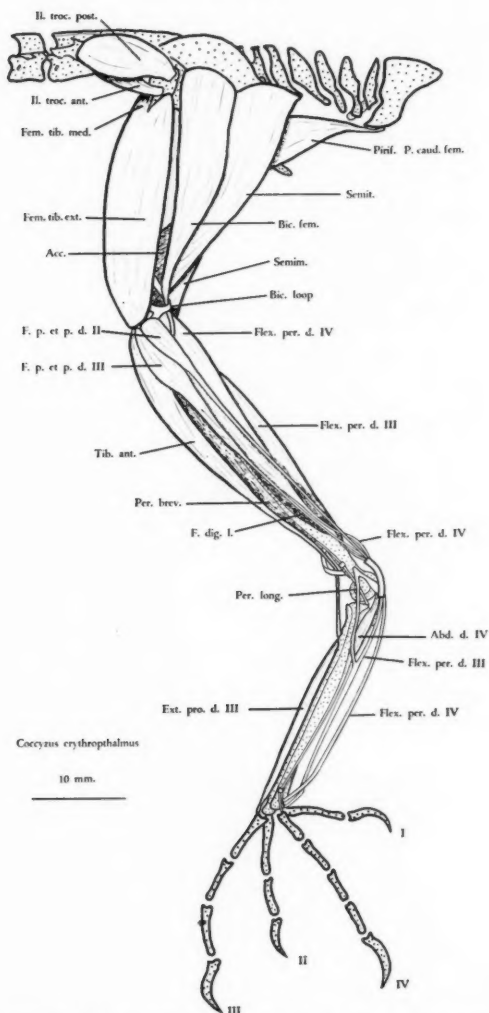
Coccyzus erythrophthalmus—Lateral view of pelvis, caudal vertebrae and left leg.

PLATE II

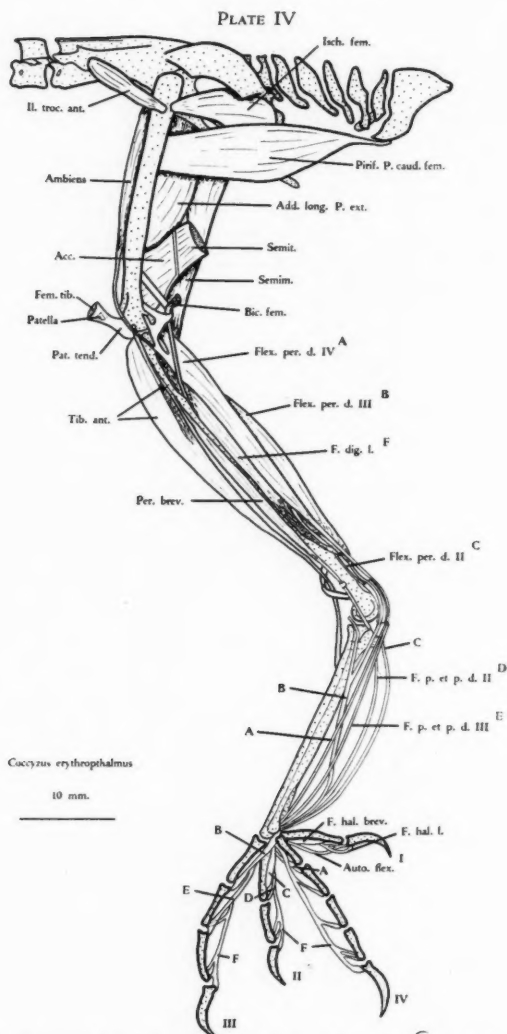


Coccyzus erythrophthalmus—Superficial muscles of the left leg (lateral view).

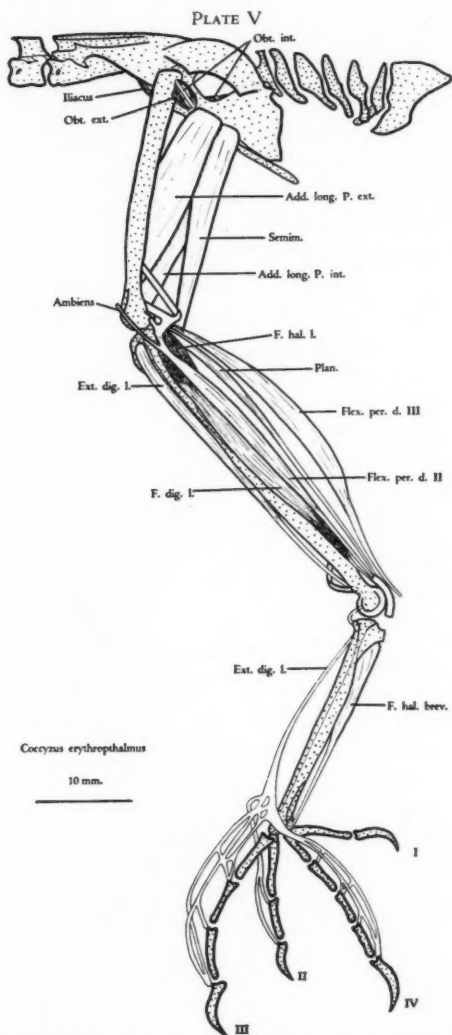
PLATE III



Coccyzus erythrophthalmus—Lateral view of the left leg showing a second layer of muscles. The following superficial muscles have been wholly or partly removed: Sar., Il. tib., Gas., Ext. brev. d. IV, Per. long.

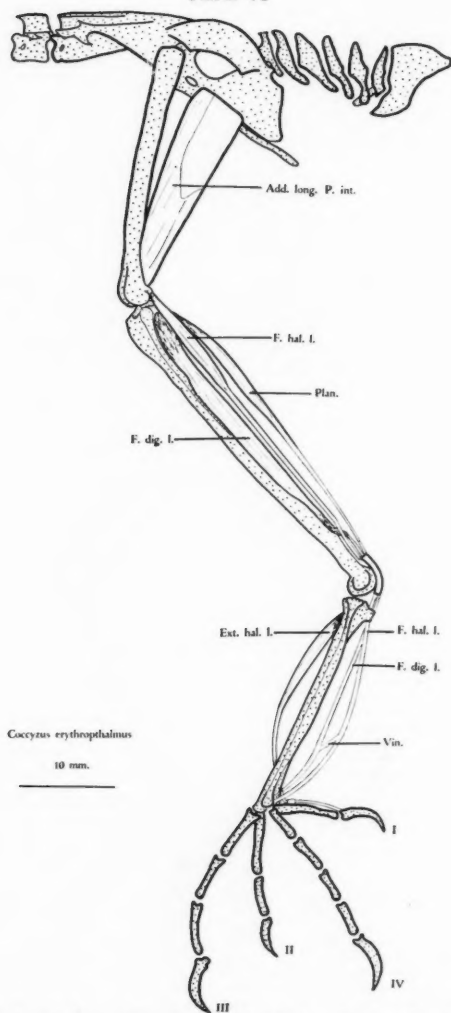


Coccyzus erythrophthalmus—Lateral view of the left leg showing a third layer of muscles. In addition to those listed for Plate III, the following muscles have been wholly or partly removed: Il. troc. post., Fem. tib. med., Fem. tib. ext., Bic. fem., Semit., Ext. pro. d. III, F. p. et p. d. II, F. p. et p. d. III, Abd. d. IV.



Coccyzus erythrophthalmus—Lateral view of left leg showing a fourth layer of muscles. In addition to those listed for Plate IV, the following muscles have been wholly or partly removed: Pirif. P. caud. fem., Acc., Ambiens, Isch. fem., Il. troc. ant., Tib. ant., Per. brev., Flex. per. d. IV.

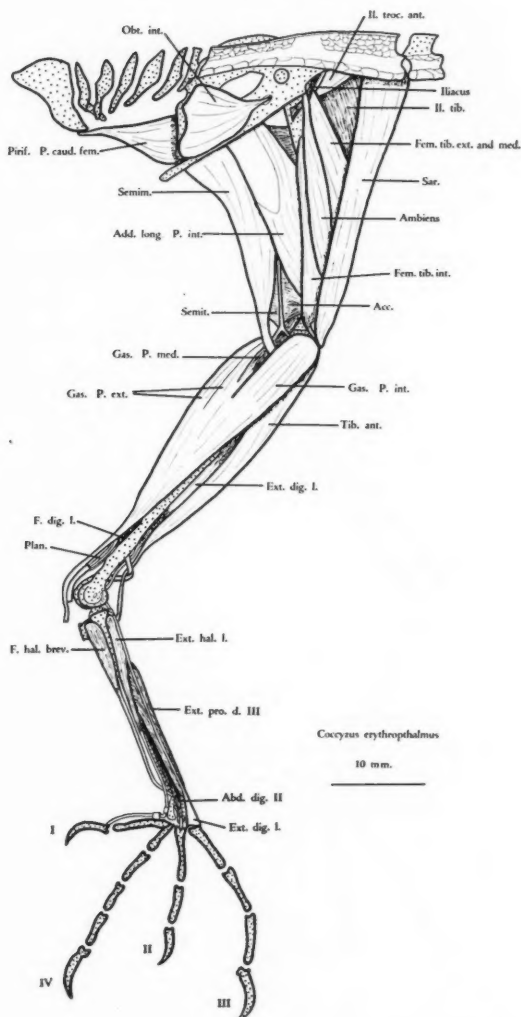
PLATE VI

*Coccyzus erythrophthalmus*

10 mm.

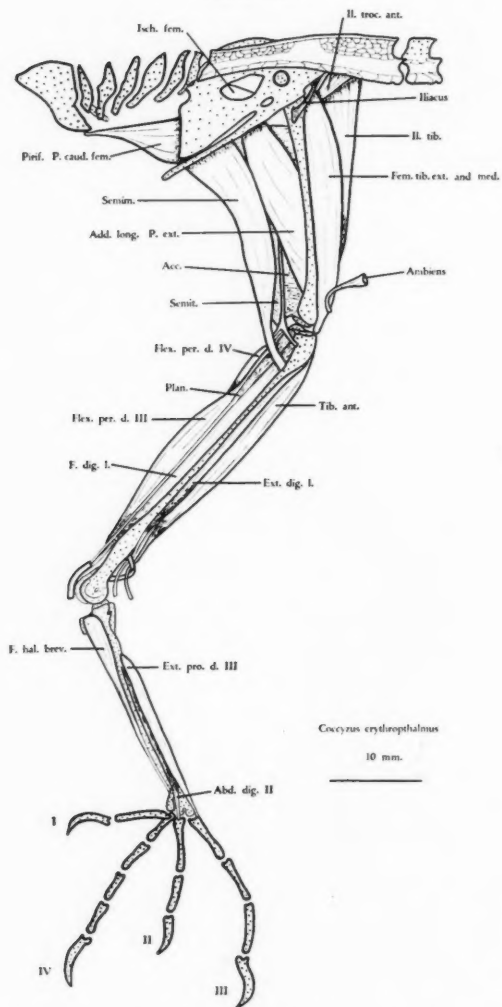
Coccyzus erythrophthalmus—Lateral view of left leg showing the deepest layer of muscles. The following additional muscles have been removed: Add. long. P. ext., Semim., Bic. fem. tendon, Flex. per. d. II, Ext. dig. I., Flex. per. d. III, Obt. ext., Obt. int.

PLATE VII



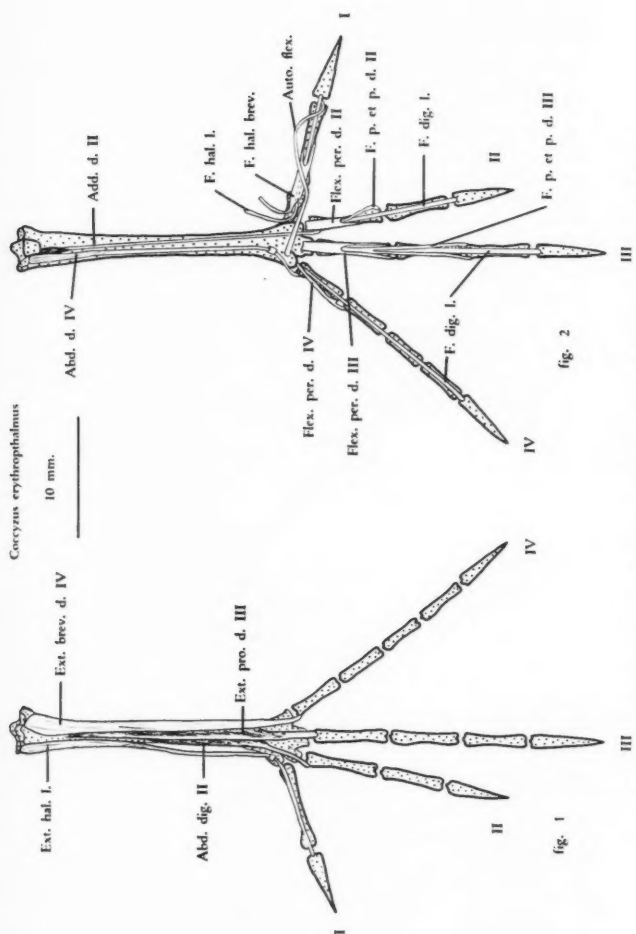
Coccyzus erythrophthalmus—Medial view of left leg showing the superficial muscles.

PLATE VIII



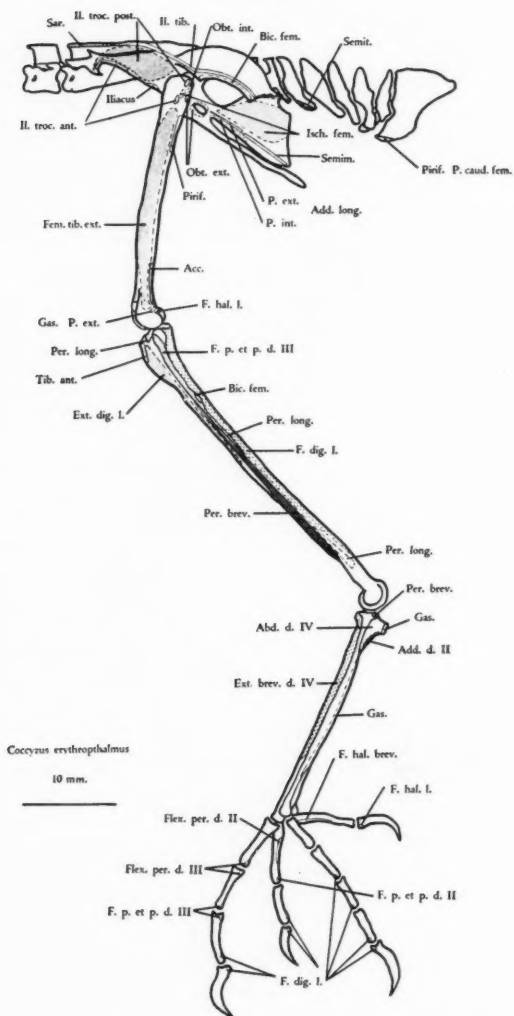
Coccyzus erythrophthalmus—Medial view of left leg showing a second layer of muscles. The following superficial muscles have been removed: Sar., Ambiens, Obt. int., Add. long P. int., Fem. tib. int., Gas., Ext. hal. l., tendon of Ext. dig. l., distal tendon of Acc.

PLATE IX



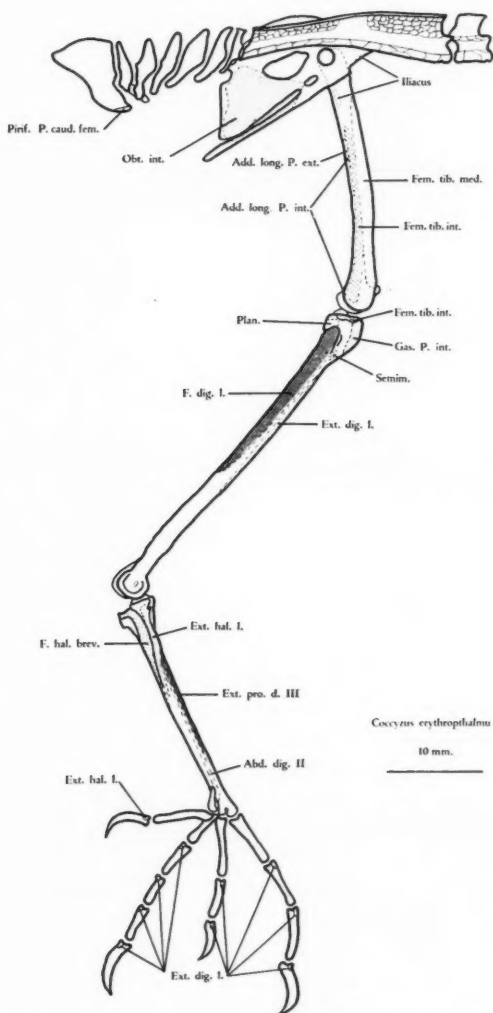
Coccyzus erythrophthalmus—Figure 1. Anterior view of tarsometatarsus and digits of left leg. Digits I and IV rotated to show extensor surface. Figure 2. Posterior view of tarsometatarsus and digits of left leg. Digits I and IV rotated to show palmar surface.

PLATE X



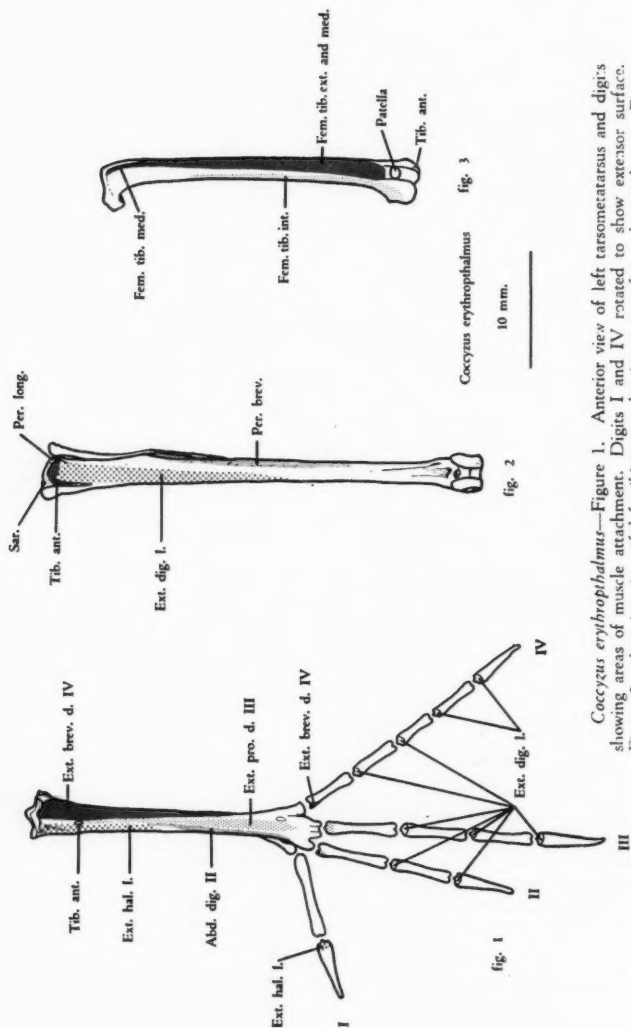
Coccyzus erythrophthalmus—Lateral view of the bones of the left leg showing areas of muscle attachment.

PLATE XI



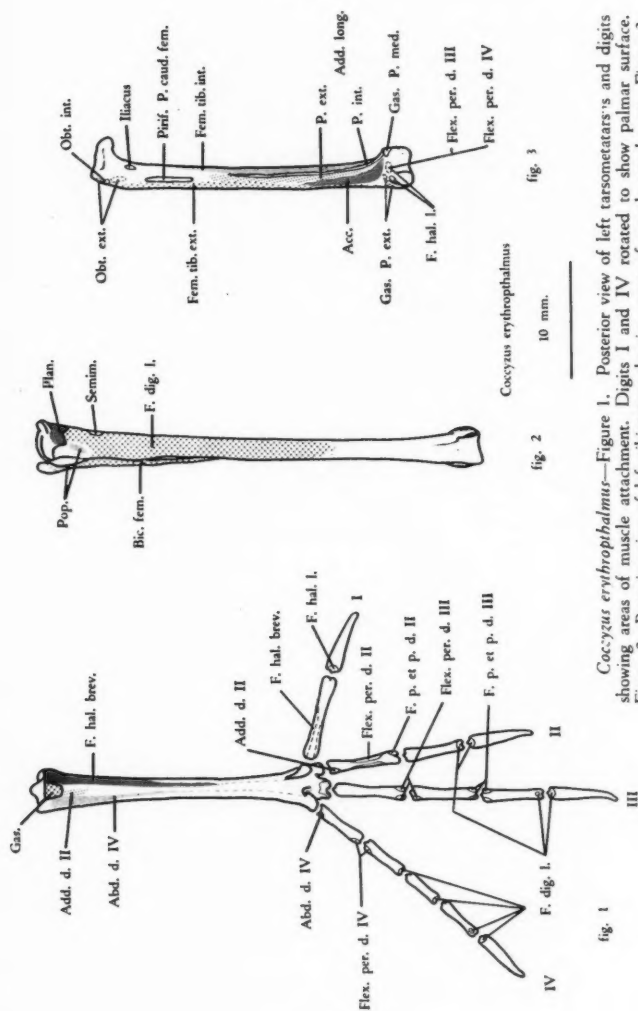
Coccyzus erythrophthalmus—Medial view of bones of the left leg showing areas of muscle attachment.

PLATE XII



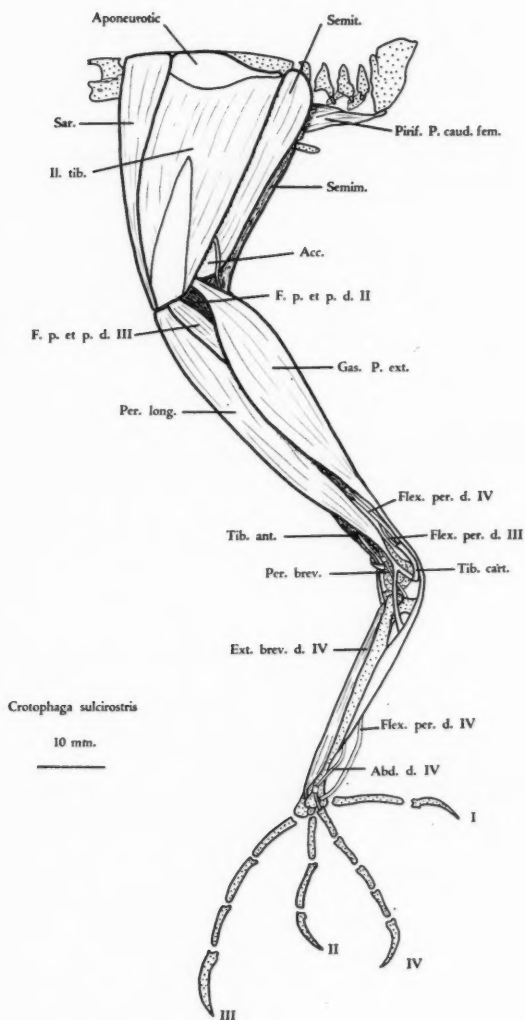
Coccyzus erythrophthalmus—Figure 1. Anterior view of left tarsometatarsus and digits showing areas of muscle attachment. Digits I and IV rotated to show extensor surface. Figure 2. Anterior view of left tibiotarsus showing areas of muscle attachment. Figure 3. Anterior view of left femur showing areas of muscle attachment.

PLATE XIII

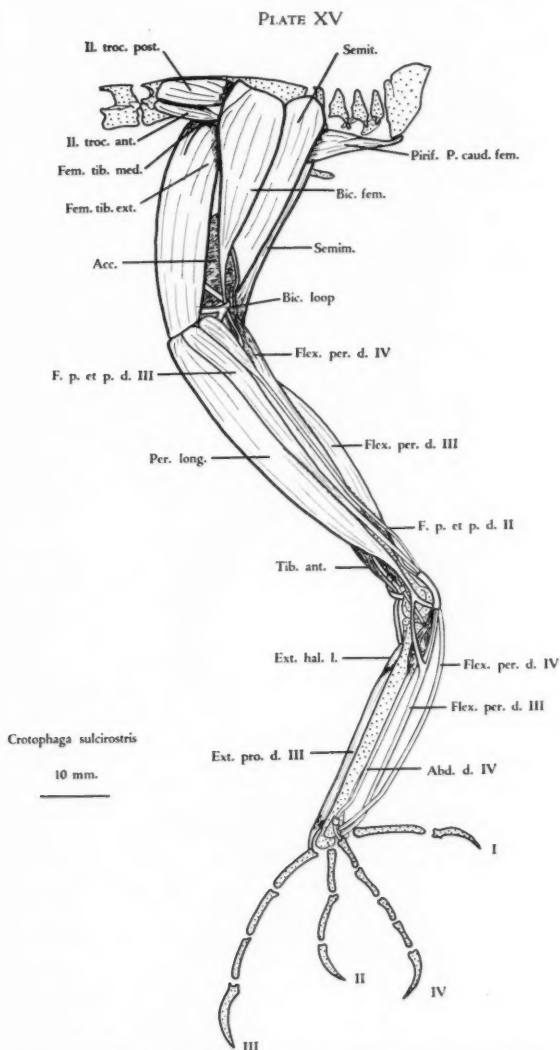


Coccyzus erythrophthalmus—Figure 1. Posterior view of left tarsometatarsus and digits showing areas of muscle attachment. Digits I and IV rotated to show palmar surface. Figure 2. Posterior view of left tibiotarsus showing areas of muscle attachment. Figure 3. Posterior view of left femur showing areas of muscle attachment.

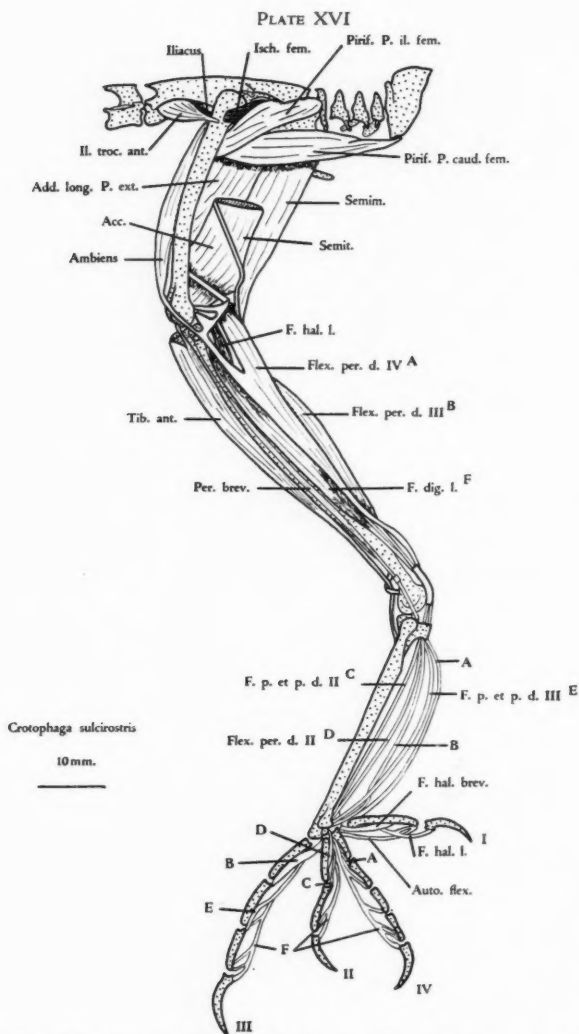
PLATE XIV



Crotophaga sulcirostris—Superficial muscles of the left leg (lateral view).

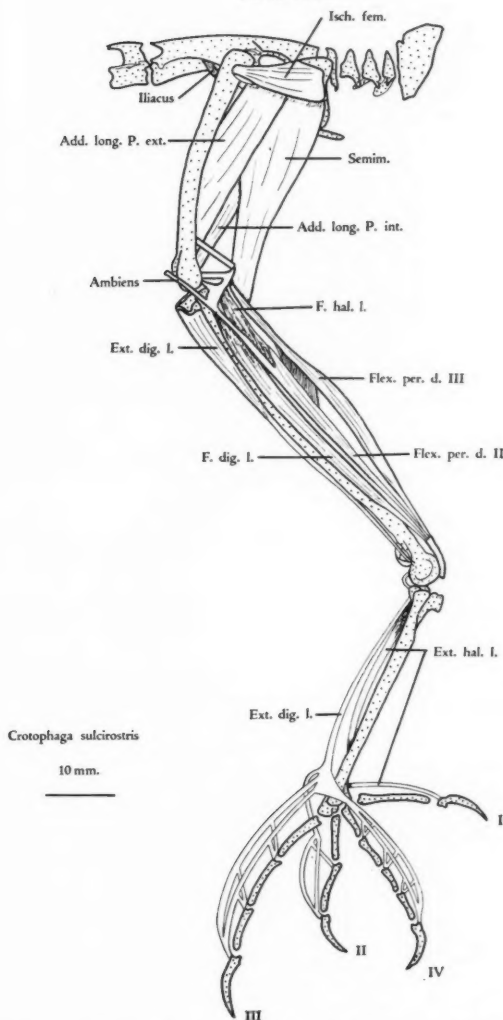


Crotophaga sulcirostris—Lateral view of left leg showing a second layer of muscles. The following superficial muscles have been wholly or partly removed: Sar., Il. tib., Gas., Ext. brev. d. IV.

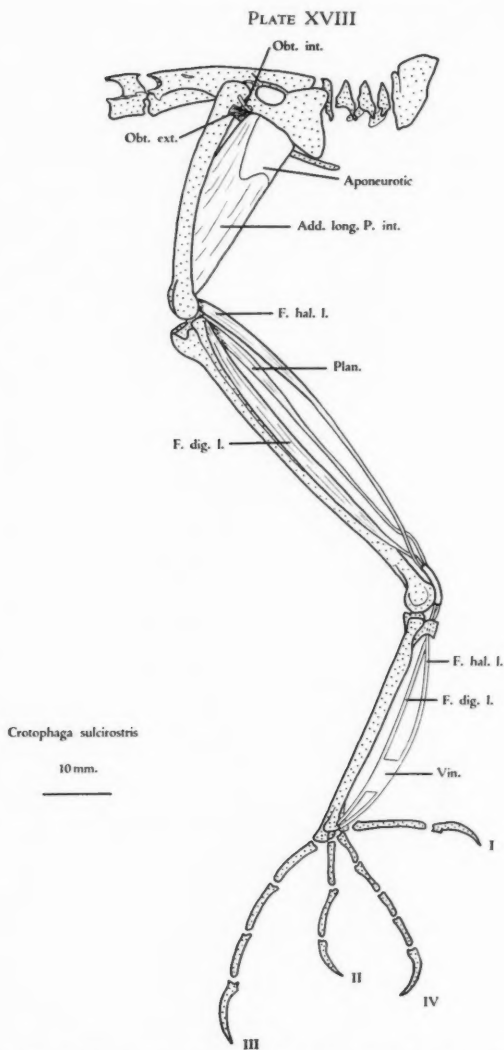


Crotophaga sulcirostris—Lateral view of left leg showing a third layer of muscles. The following additional muscles have been removed: Il. troc. post., Fem. tib. med., Fem. tib. ext., Bic. fem., Semit., Per. long., Ext. pro. d. III, F. p. et p. d. II, F. p. et p. d. III, Abd. d. IV.

PLATE XVII

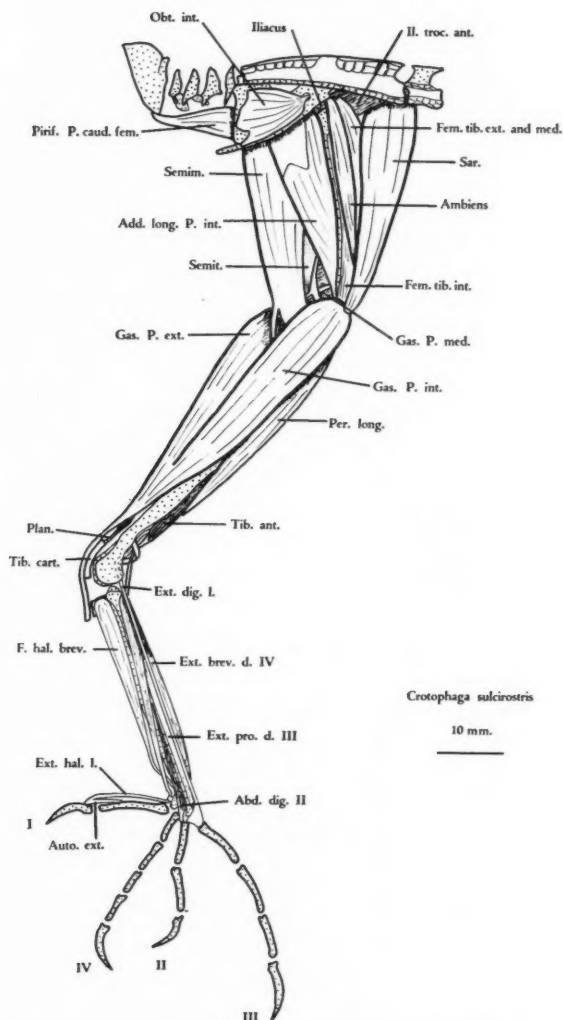


Crotophaga sulcirostris—Lateral view of left leg showing a fourth layer of muscles. The following additional muscles have been removed: Pirif. P. caud. fem., Acc., Ambiens, Il. troc. ant., Tib. ant., Per. brev., Flex. per. d. IV.

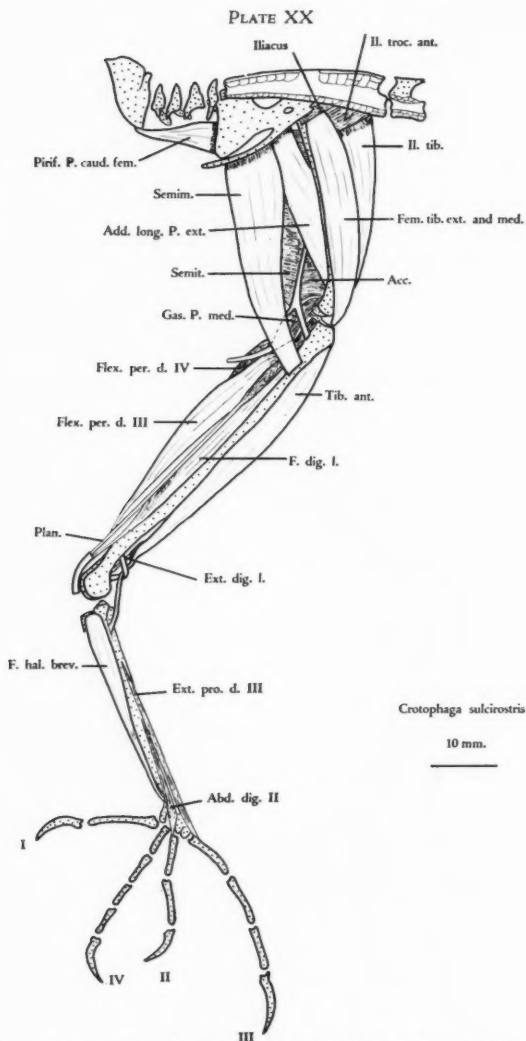


Crotophaga sulcirostris—Lateral view of left leg showing the deepest layer of muscles. The following additional muscles have been removed: Add. long. P. ext., Semim., Bic. fem. tendon, Isch. fem., Flex. per. d. II, Flex. per. d. III, Ext. dig. I.

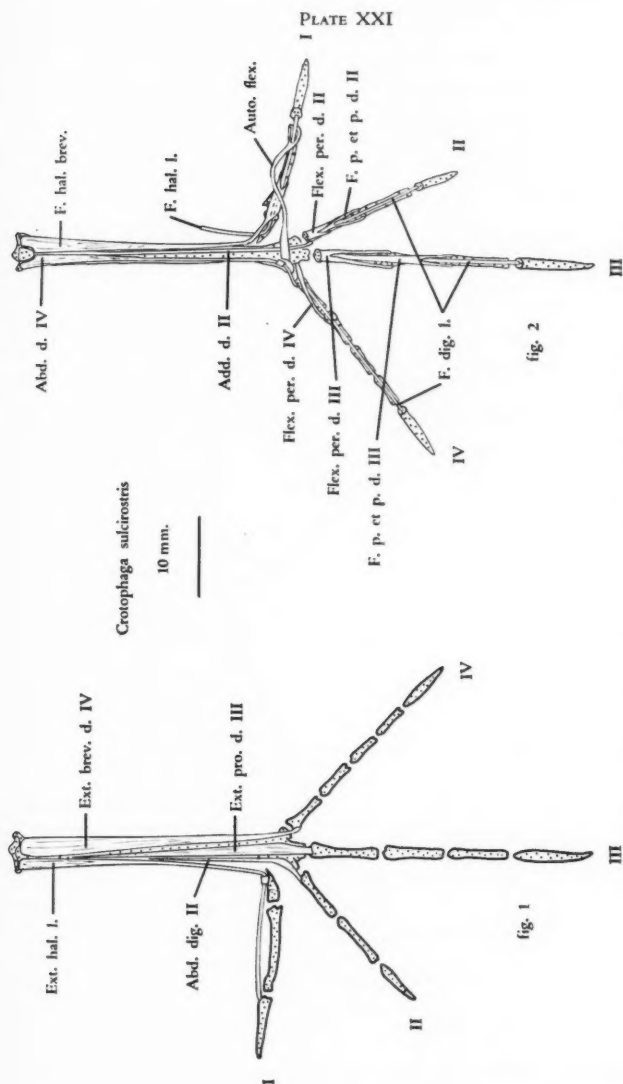
PLATE XIX



Crotophaga sulcirostris—Medial view of left leg showing the superficial muscles.

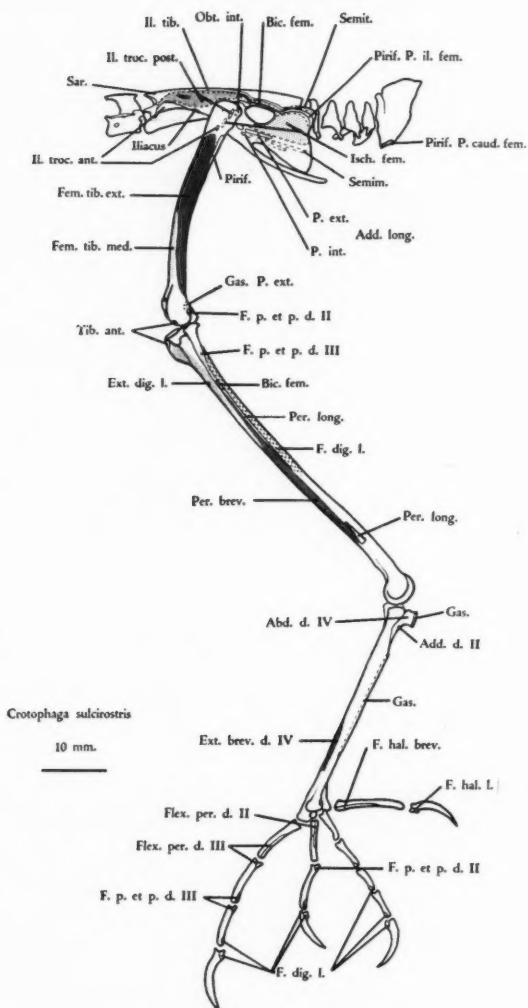
*Crotophaga sulcirostris*

Crotophaga sulcirostris—Medial view of left leg showing a second layer of muscles. The following superficial muscles have been removed: Sar., Ambiens, Obt. int., Add. long. P. int., Fem. tib. int., Gas. P. ext. and P. int., Per. long., Ext. hal. l., tendon of Ext. dig. l., Ext. brev. d. IV.



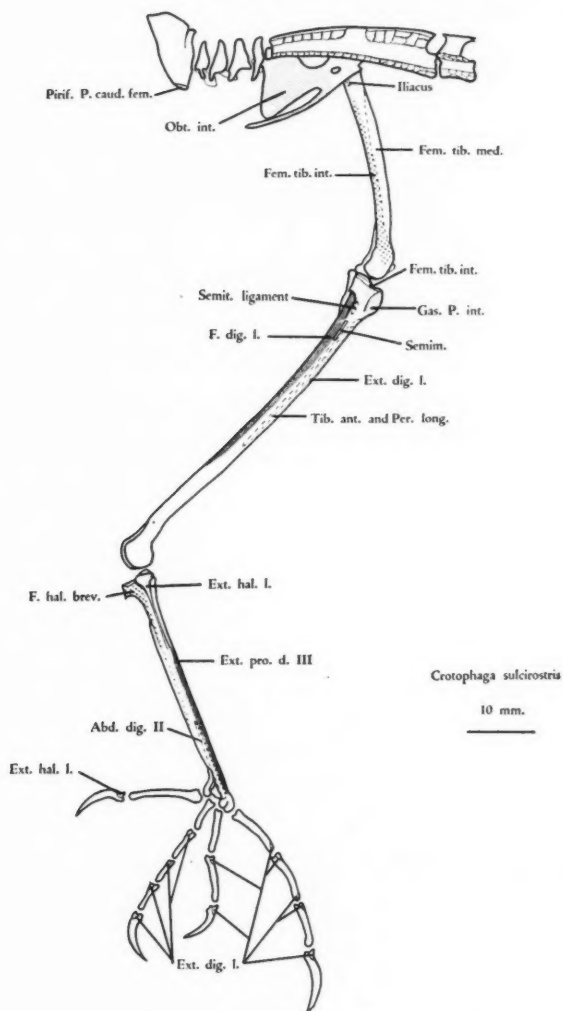
Crotophaga sulcirostris.—Figure 1. Anterior view of left tarsometatarsus and digits. Digits I and IV rotated to show extensor surface. Figure 2. Posterior view of left tarsometatarsus and digits. Digits I and IV rotated to show palmar surface.

PLATE XXII



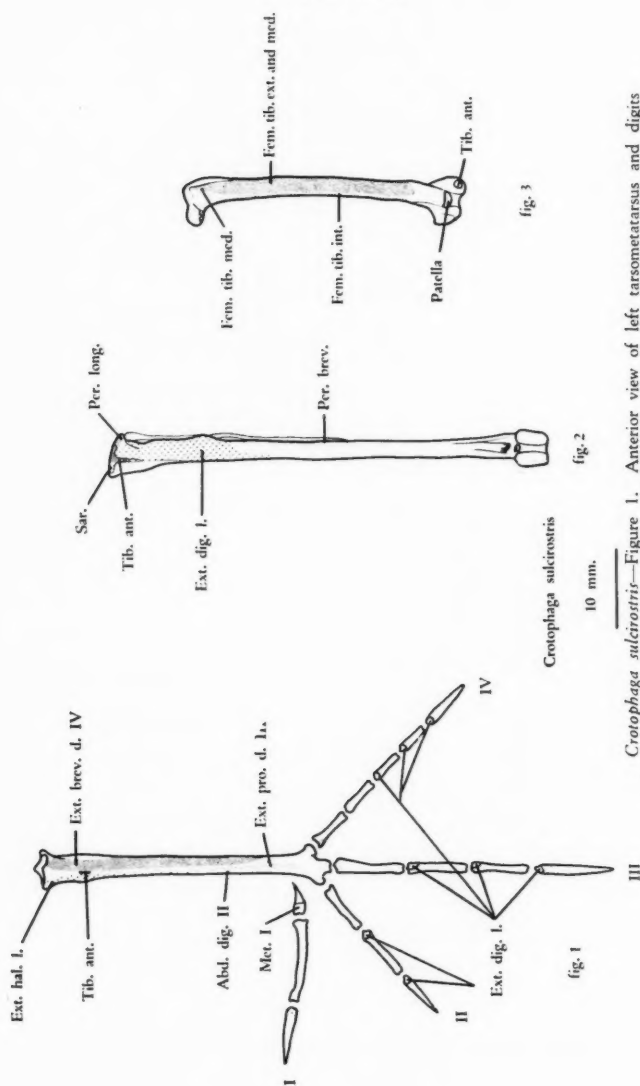
Crotophaga sulcirostris—Lateral view of the bones of the left leg showing areas of muscle attachment.

PLATE XXIII



Crotophaga sulcirostris—Medial view of bones of the left leg showing areas of muscle attachment.

PLATE XXIV

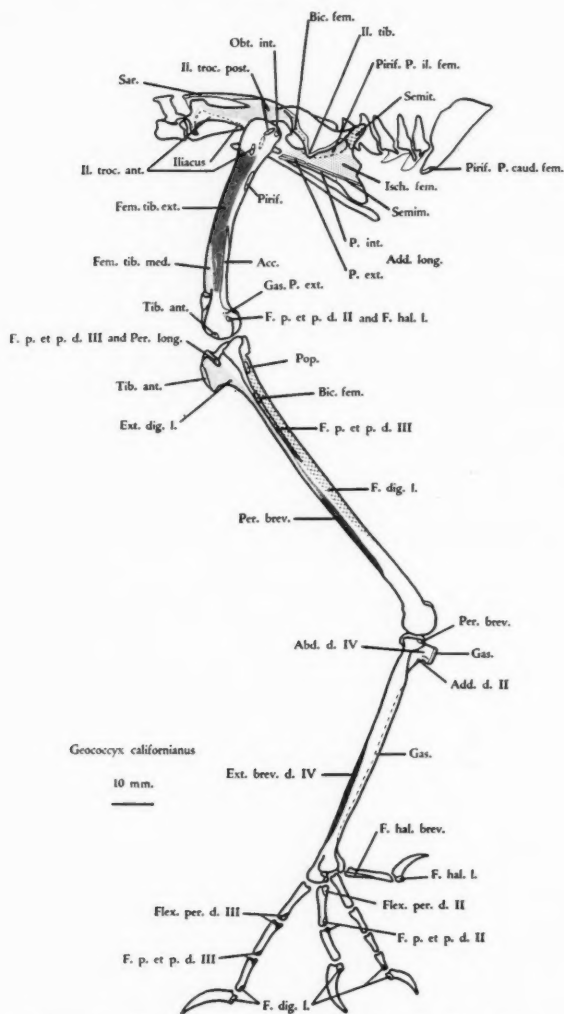


Crotophaga sulcirostris.—Figure 1. Anterior view of left tarsometatarsus and digits showing areas of muscle attachment. Digits I and IV rotated to show extensor surface. Figure 2. Anterior view of left tibiotarsus showing areas of muscle attachment. Figure 3. Anterior view of left femur showing areas of muscle attachment.

[illegible]

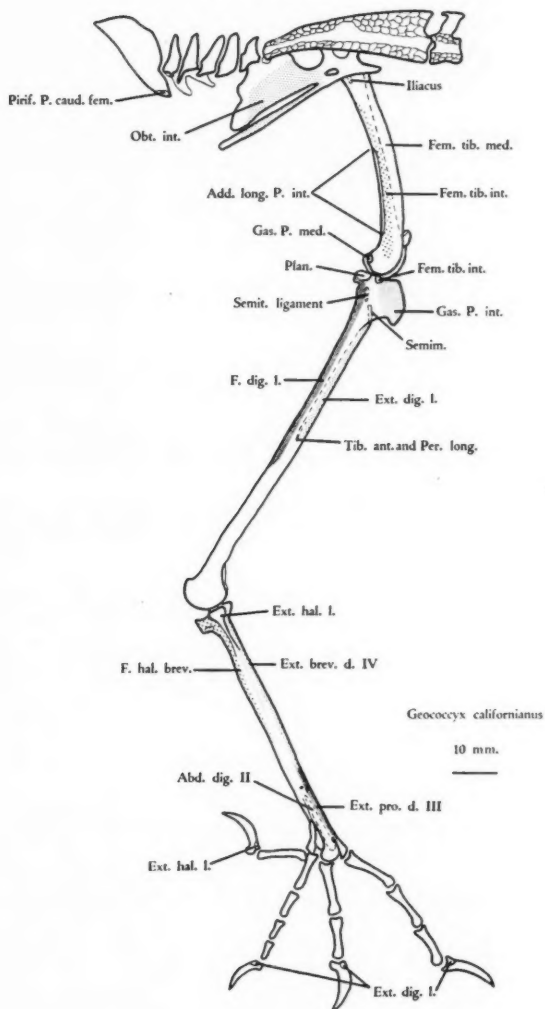
Crotophaga sulcirostris—Figure 1. Posterior view of left tarsometatarsus and digits showing areas of muscle attachment. Digits I and IV rotated to show palmar surface. Figure 2. Posterior view of left tibiotarsus showing areas of muscle attachment. Figure 3. Posterior view of left femur showing areas of muscle attachment.

PLATE XXVI



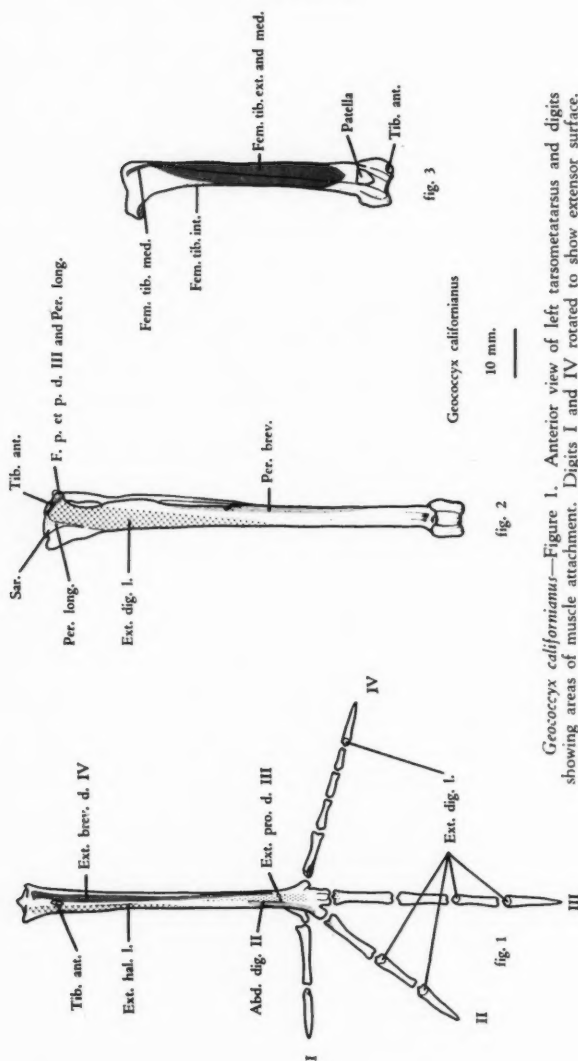
Geococcyx californianus—Lateral view of bones of left leg showing areas of muscle attachment.

PLATE XXVII



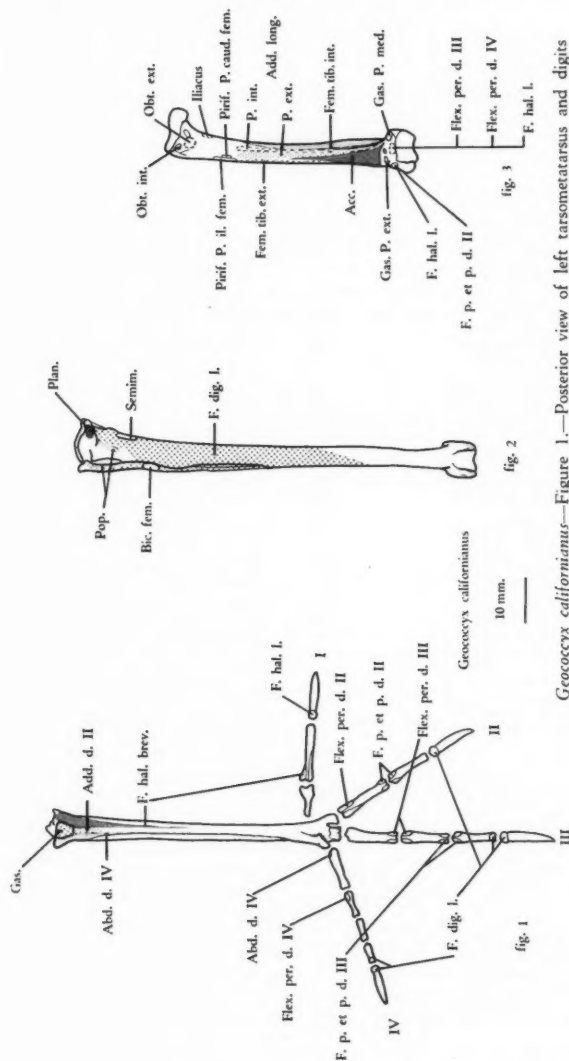
Geococcyx californianus—Medial view of bones of left leg showing areas of muscle attachment.

PLATE XXVIII



Geococcyx californianus—Figure 1. Anterior view of left tarsometatarsus and digits showing areas of muscle attachment. Digits I and IV rotated to show extensor surface. Figure 2. Anterior view of left tibiotarsus showing areas of muscle attachment. Figure 3. Anterior view of left femur showing areas of muscle attachment.

PLATE XXIX



Geococcyx californianus—Figure 1.—Posterior view of left tarsometatarsus and digits showing areas of muscle attachment. Digits I and IV rotated to show palmar surface.
Figure 2. Posterior view of left tibiotarsus showing areas of muscle attachment. Figure 3. Posterior view of left femur showing areas of muscle attachment.

A Study of the Breeding Biology of the Purple Martin (*Progne subis*)

Robert W. Allen*

Margaret M. Nice

5727 Harper Avenue, Chicago 37, Illinois

CONTENTS

Introduction	606	Comparison with other swallows	629
Migration	607	The young in the nest	632
Spring migration	607	Development of the young	632
Fall migration	613	Length of fledging	633
Nesting sites	614	Brooding	634
Natural nesting sites	614	Sanitation	634
Man-made sites	615	Feeding	634
Nesting populations in		Nesting success	636
Ann Arbor and Blue Island	616	Nesting success at	
Recommendations for martin houses	616	the George Reserve	637
Territory and pair formation	617	Nesting success of	
The male selects a nesting territory	617	martins in three studies	637
The male selects a room	618	Success of hole-nesting	639
The pre-nuptial period	619	Factors inimical to	
Sex discrimination	619	nesting success of the martin	641
Nest building	619	Survival problems of adult martins	647
Building the nest	619	Weather	647
Copulation and sexual fighting	621	Predators	648
The nests	621	Destruction by man	649
Egg laying	623	Banding purple martins	650
The eggs	623	Banding adult martins	650
Number of broods	624	Banding young martins	652
Re-nesting	625	Return of young to the birthplace	653
Incubation	625	The martin as a social bird	655
Length of incubation	625	Migration and roosting	656
Percentage of time		Nesting behavior	656
the eggs were covered	626	Asocial behavior	658
Duration of attentive periods	626	Summary	659
Duration of inattentive periods	627	References	660
The role of the male	629		

Introduction

The Purple Martin, a beautiful, musical, abundant bird, now largely dependent on man's hospitality, has been strangely neglected as a subject of study. Over sixty years ago Otto Widmann (1884) made important observations on the nesting and roosting of this species near St. Louis. A few years (1903, 1909) later Joseph W. Jacobs published two popular accounts of the growth of his colony in Waynesburg, Pennsylvania. The way was clear for a modern life history study when Robert Allen started on the project in

* Robert Allen lost his life in New Guinea in October 1943 while serving with the Armed Forces of the United States.

1938 at the University of Michigan under the direction of Dr. Josselyn Van Tyne.

His faithful, day by day observations on life in the colonies on territory, pair formation, territorial and sexual fighting form a major contribution to our knowledge of the life history of this bird. He settled several controversial points, such as the number of broods, length of incubation and which sex incubates. He gave a clear picture of the status of the Martin and its nest competitors at the present day in Michigan. He compared his findings with those published on other swallows. All of the charts in the present paper are his except Numbers 2, 3 and 9. Direct quotations from his manuscripts are enclosed in quotation marks followed by his initial.

In working up this thesis for publication, I have been hampered by the absence of most of the original notes. On the other hand, I have had the advantage of a decade of further publications on swallows, including Alexander Sprunt's account of the Martin (Bent, 1942), of additional banding returns, and of generous assistance from many correspondents, especially in regard to migration dates. Some points in which I have been particularly interested are: the early history of the Martin—its relation to nest competitors, to avian predators, to man, and to weather; the relation of temperature to Martin migration, start of nesting, and survival; and the return of the young to the birth place. Comparisons have been made with nesting success of 14 other hole-nesting species and with the breeding biology of 13 other species of swallows. Except for Number 7, the tables in the article are my responsibility.

It is a privilege to acknowledge the help of many people who have kindly given me information. Their names appear on many of the following pages. Thanks are due to Dr. Josselyn Van Tyne for advice and assistance and a final reading of the manuscript. I am particularly indebted to Mr. William Stickel for his keen interest in all problems connected with the paper, his enlistment of aid from the Fish and Wildlife Service at the Patuxent Research Refuge in typing, and in preparation of the charts, and for his constructive criticism of the manuscript.—MARGARET M. NICE.

Migration

The Purple Martin, *Progne subis subis* (Linnaeus), arrives early in the spring and leaves early in the fall.

SPRING MIGRATION

Some Martins, usually adult males, arrive very early in the spring. Some colonies are definitely earlier than others, this situation continuing year after year. First year birds typically come later than older birds, sometimes several weeks later.

Migration in Ann Arbor.—"In 1938 the first Martins in the vicinity of Ann Arbor were reported by two individuals on the 29th of March, while a

third person reported them on the 30th. A cool period began on the 1st of April and I had no further reports of birds until the 12th of that month when several appeared at the George Reserve colony. After that the Martins came rapidly until the 6th of May, when all were present in the one colony of which I kept close track. The majority arrived the middle of April.

"When a cold period follows the arrival of the first birds they usually disappear for a time. I am not sure whether they die or retreat south. Some of them died in early April of 1938 and it is probable that many more did. Certain large colonies are usually the first to be visited each year. Some of the first birds to arrive seem exhausted; they sit for a long time without moving, with wings drooped as though unable to hold them up." (A.)

Occasionally Martins do retreat south again. In the Chicago region on March 26, 1950 there was a strong eastsoutheast wind with a mean temperature 13° F. above normal, on March 27 a strong southwest wind, mean temperature 14° above normal; on the 27th a remarkable number of birds of many species had arrived. On the 28th the wind had changed to westsouthwest, the temperature was 4° below normal; the next day with a strong northnorthwest wind it had dropped to 11° below normal. About 8 on the morning of the 27th James Decker saw a number of birds, several Martins among them, flying south, 10 to 14 hours before the advent of the cold front.

Williams (1950: 58) writes: "In late afternoon on March 22, 1947 I saw several large flocks of Ring-billed Gulls, *Larus delawarensis*, many Bank Swallows, *Riparia riparia*, and a few Chimney Swifts, *Chaetura pelagica*, and Purple Martins, *Progne subis*, migrating southeastward into a brisk and warm southeast wind. The first warm wave of the spring had surged up from the south a day or two previously, had occupied all the Gulf States, and had ascended the Plain States as far as northern Nebraska. At the same time, however, a cold front was just entering the northwest corner of the United States. But this cold front did not reach Houston till about 40 hours after I had seen the birds migrating southeast."

The owner of the largest colony of Martins in Ann Arbor furnished first arrival dates for 1932 to 1935, 1937 and 1938; they ranged from March 28 to April 7, averaging April 1. This was an exceptionally early colony. In figure 1 the date of arrival each year is shown in relation to daily mean temperature.

Excess temperature during the last half of March brought the birds on the 28th and 29th in 1935 and 1938, but never earlier, no matter how high the thermometer might have risen during the third week of the month. Temperatures not far from normal during the last half with a rise at the end of the month brought the birds on the 30th and 31st in 1932 and 1933. Markedly low temperatures during the last half of March in 1934 and 1937 delayed the birds until the first week of April.

In table 1 the six years are arranged in order of earliest arrival; the mean temperatures of the day of arrival and of the last 10 days of March are given along with the departure from normal.

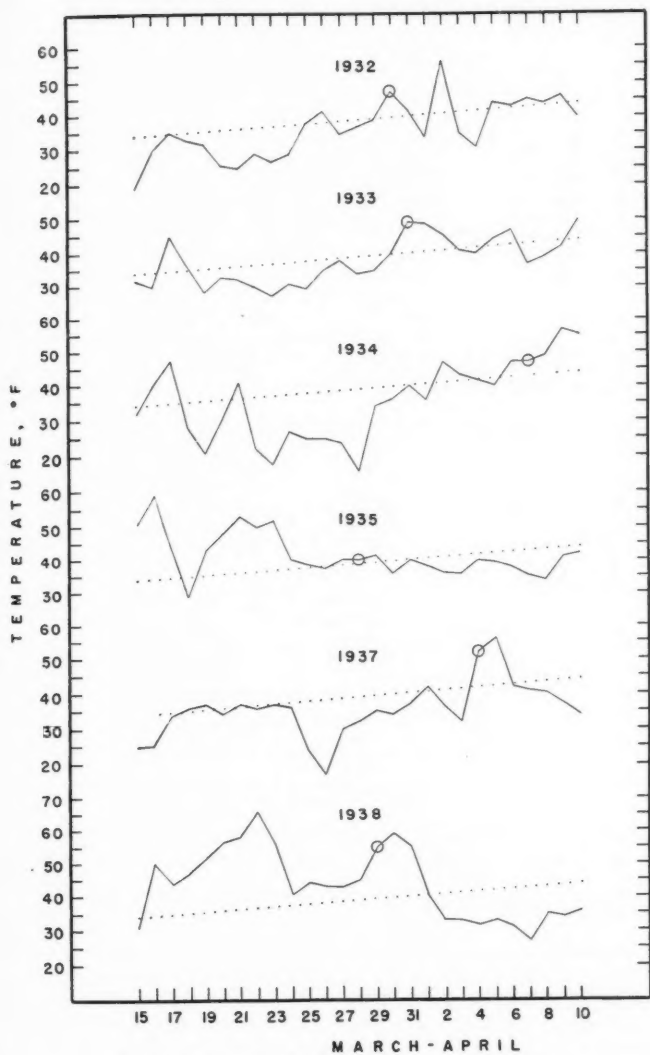


Fig. 1.—Migration and daily temperature at Ann Arbor

TABLE 1.—Arrival of purple martins at a very early colony in Ann Arbor

Year	Date	Temperature	Mean Temperature		Last 10 Days of March Departure from normal
			Day of Arrival	Temperature	
			Departure from normal		
1935	Mar. 28	40.5°	+ 2.1	42.3°	+ 2.6
1938	Mar. 29	55.1°	+14.7	50.9°	+11.2
1932	Mar. 30	48.7°	+10.7	36.5°	— 3.2
1933	Mar. 31	49.6°	+ 8.9	35.2°	— 4.5
1937	Apr. 4	52.6°	+10.3	33.4°	— 6.3
1934	Apr. 7	47.0°	+ 7.0	26.6°	—13.1
Average	Apr. 1	48.9°	+ 8.9	37.5°	— 2.2

In figure 2 much of the same material is shown arranged chronologically.

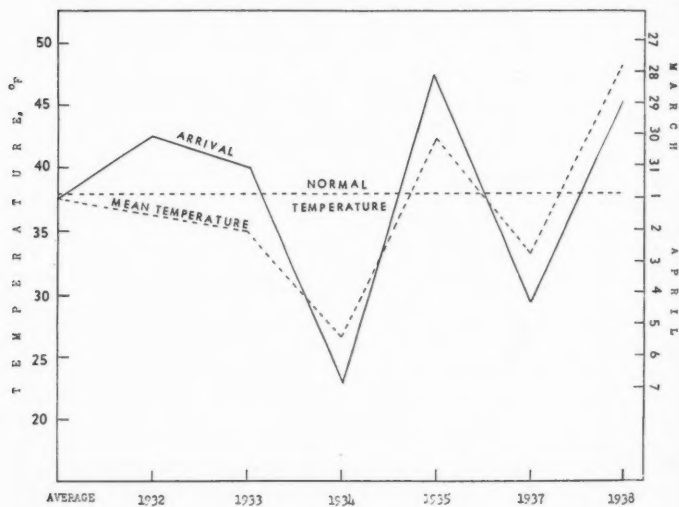


Fig. 2.—Average mean temperature of the last ten days of March and first arrival of Purple Martins at Ann Arbor

A striking correlation is shown between migration and temperature. When the temperature of the last ten days of March averaged 3° to 11° F. above normal, the birds arrived on March 28 and 29; when it averaged 3° to 5° below normal they arrived March 30 and 31; when it averaged 6° to 13° below

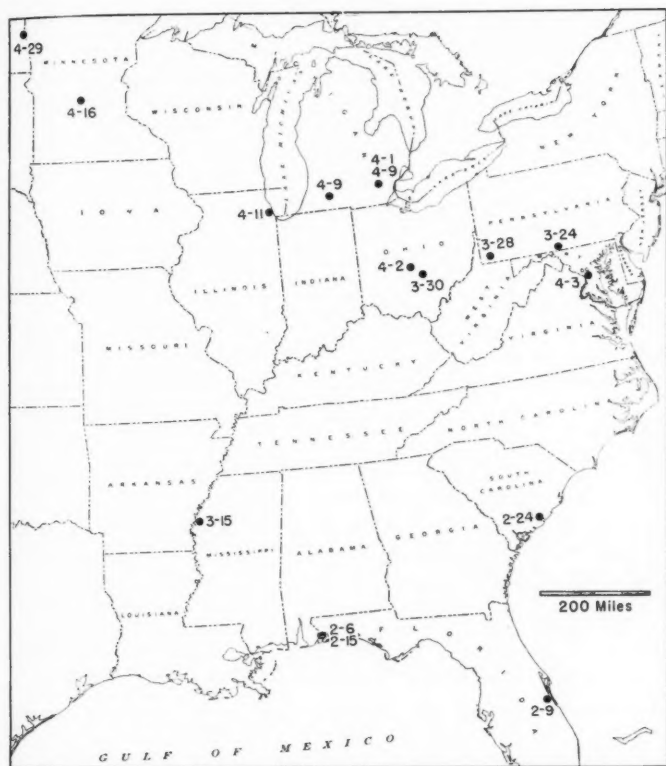


Fig. 3.—Progress of spring migration with the Purple Martin

normal, they did not come until April 4 and 7. The mean temperature of the day of arrival ranged from 2° to 15° above normal, averaging 9° ; or if 1935 is omitted, from 7° to 15° , averaging 10° . In 1935 the Martins seem to have been influenced by the high temperatures from March 15 to 24 and probably had come further north than usual by that time.

With the Song Sparrows, *Melospiza melodia* in Columbus, Ohio, there was a definite temperature threshold (Nice, 1937: 47-48) during the six years of observation. This is not so clear with the Martins, partly because of the comparatively low temperature of April 28, 1935. However, when we consider the average mean temperature of the week before arrival at Ann Arbor, we find that these temperatures ranged from 38° to 47° F., averaging 42.7° for the three earliest arrivals, and 36.8° to 38.8° , averaging 37.7° for the three

latest. Hence migration occurred at higher average temperatures with the earlier arrivals than with the later ones.

Migration and Temperature in Four Localities.—The relationship between average date of arrival and average mean temperature is shown in table 2 for four localities in north central United States.

TABLE 2.—Average dates and mean temperatures of day of arrival in four localities

Locality	Dates		Date of Arrival		Temperature Day of arrival	Temperature Week before arrival
			Range	Av.	Av. Departure	Av. Departure
Ann Arbor, Mich.	'32-'38	6	3/28-4/7	4/1	49° + 9	40° -0.1
Chicago, Ill.	'29-'43	14	4/2 -4/20	4/11	56° +11	45° +7
Lancaster, Ohio	'39-'48	8	3/26-4/5	3/30	58° +14	50° +7
Columbus, earliest	'41-'48	5	3/30-4/6	4/2	51° + 5	51° +6
Became common	'41-'48	6	4/9 -4/13	4/11	49° 0	51° +2.5

The data for Chicago are based on 14 years' observation in Lincoln Park by William Dreuth (see Clark and Nice, 1950); those for Lancaster, Ohio on records of Charles R. Gosling, and those for Columbus on records of the Wheaton Club, all Ohio dates being furnished by Dr. Edward S. Thomas. The Ann Arbor colony was very early, and the Lancaster colony early, while the others are probably more typical of the majority of colonies. The main migration in Columbus averaged nine days later than the first arrival.

The temperature of the day of arrival at the two early colonies averaged 9° and 14° F. above normal; at the two more typical colonies 5° and 11°, with the main migration coming at normal temperatures. As to temperatures the week before migration, these averaged 40° to 50° for all localities. This (40°) corresponded to normal temperature for Ann Arbor, while for the next three stations the weekly average (45° to 51°) was 6° to 7° above normal per day. For the main migration the average came to 2° above normal per day.

Migration Dates from Florida to North Dakota.—Purple Martins may arrive in January in Florida (Howell, 1931: 334) and Louisiana (Oberholser, 1938: 414). The gradual northward movement is shown by a series of migration dates (based on 6 to 55 years' observation) from 13 localities in eastern United States in figure 3 and table 3.

The average arrival in Florida falls in early February; at Charleston, South Carolina, in late February; in northwestern Mississippi mid March; in Pennsylvania and southern Ohio, late March; in Washington, D. C., central Ohio and Ann Arbor, the first of April; in Chicago and southern Michigan,

mid April; in Fargo, North Dakota, the last of April. Irregularities in the record are explainable by the peculiar nature of Martin migration. For two localities—Pensacola and Ann Arbor—we have dates for very early and more typical colonies; the early ones averaged eight and nine days earlier than the others. The Greencastle, Pennsylvania, colony seems also to have been an early one. The data from Washington, D. C., covering 55 years, probably include both early and more typical colonies.

TABLE 3.—Average arrival dates of martins in thirteen localities

Locality	Lat.	Long.	Years	Dates	Range	Average	Authority
Melbourne, Fla.	28° 4'	81° 40'	12			2/9	Howell, 1932
Pensacola, Fla.							
Early	30° 20'	87° 15'	9	'42-'50	2/4 -2/15	2/6	Weston, F. M.*
"Typical"			16	'25-'41	2/3 -2/22	2/15	Weston, F. M.*
Charleston, S. C.	32° 45'	80°	8	'91-'07	2/16-2/29	2/24	Wayne, 1910
Rosedale, Miss.	33° 50'	91°	6	'43-'49	3/2 -3/25	3/15	Vaiden, M. G.*
Washington, D. C.	38° 55'	77°	55	'82-'48	3/13-4/24	4/3	Robbins, S. C.*
Greencastle, Pa.	39° 45'	77° 40'	8	'15-'22	3/8 -4/8	3/24	Ziegler, 1923
Waynesburg, Pa.	39° 52'	80° 20'	11	'91-'02	3/20-4/9	3/28	Jacobs, 1903
Lancaster, Ohio	39° 40'	82° 40'	8	'39-'48	3/26-4/5	3/30	Goslin, C. R.*
Columbus, Ohio	40°	83°	5	'41-'48	3/30-4/6	4/2	Thomas, E. S.*
Ann Arbor, Mich.	42° 25'	84°	6	'32-'38	3/28-4/7	4/1	Allen, R. W.
Ann Arbor, Mich.	42° 25'	84°	25	'06-'30	3/16-4/18	4/9	Wood, 1934
Vicksburg, Mich.	42° 15'	85° 45'	30	'96-'26	3/24-4/8	4/9	Rapp, 1926a
Chicago, Ill.	41° 47'	87° 44'	14	'29-'43	4/2 -4/20	4/11	Dreuth, W.
Litchfield, Minn.	45° 8'	95° 30'	13	'12-'24	4/9 -5/1	4/16	Roberts, 1932
Fargo, N. D.	46° 50'	96° 50'	36	'10-'49	4/15-5/15	4/29	Stevens, 1950

* Information by letter.

FALL MIGRATION

Soon after the single brood is on the wing, the birds start on their leisurely way south. Bent (1942) gives late dates of departure from Seattle, Quebec and New Brunswick to Louisiana and Florida; these all come in September and October. Howell (1932) mentions a few in November. Molting occurs after the Martins have reached their winter quarters in Brazil.

Martin Roosts.—In regions where Martins are fairly common they may gather in fall in immense roosts of as many as 100,000 birds. At times such congregations interfere with human interests and attempts are made to rout the birds with fireworks, water, clubbing and shooting. Such roosts have been described for Chicago (Craigmile, 1939), (Wright, 1939), for Buckeye Lake, Ohio (Trautman, 1940), North Carolina (Dutcher, 1920), South Carolina (Wayne, 1910), Florida (Fisher, 1907), Cape May, New Jersey (Stone, 1937) the Mississippi River near St. Louis (Widmann, 1922) and

eastern Kansas (Linsdale, 1928), the last three descriptions being especially impressive.

At Tucson, Arizona the southwestern Martins, *Progne subis hesperis*, congregate in a common roost from their arrival in May to their departure in September. "During the summer months," writes Cater (1944) "the number at the roost, an estimated 3000, did not change noticeably, except during the egg-laying and incubating periods, which in this region begin the last week in June and continue until the last week in July." During this period males greatly outnumbered females. By Sept. 22, an estimated 13,000 birds were using the roost (see also Anderson, 1946).

Nesting Sites

Purple Martins nest in cavities, usually colonially. Originally they must have depended largely on abandoned Woodpecker holes in trees. This they still do to a large extent in the West, but in the East, where the primeval forests are gone, they depend almost entirely on man-made structures.

NATURAL NESTING SITES

In the East, scattered instances of nesting in the wild are reported as late as 1940 in Florida (Bent, 1942), and Georgia (F. W. Hebard, letter), and 1950 in New Jersey (Fables, 1950). Formerly they were recorded from South Carolina in cypresses (Bent, 1942), and from Alabama (Howell, 1924), New England (Forbush, 1929), Michigan (Barrows, 1912), Iowa (Anderson, 1907), and other states in the East and Middle West. In Ohio they nested in cavities in elm, oak and walnut (Wheaton, 1879) and in stumps in a reservoir (Jones, 1903). In Minnesota large colonies were found nesting under boulders on Spirit and Hennepin Islands in 1886, 1919, and 1930 (Roberts, 1932).

West of the Hundredth Meridian *Progne subis subis* still habitually uses abandoned Woodpecker holes and natural cavities. It nests in great dead pines in New Mexico (Bailey, 1928), in the mountains of northeastern Arizona (Coues, 1878; Mearns, 1890) and southeastern Arizona (Kimball, 1921), in California (Van Rossem, 1914), and Oregon (Gabrielson and Jewett, 1940). It has also been found in old spruce snags in Oregon, in sycamores in California (Grinnell and Storer, 1924), and in aspens of the coniferous forests in Utah (Woodbury et al., 1949). Most observers mention "several" pairs to one tree. Definite numbers range from four in New Mexico to twenty in California (Van Rossem, 1914).

The Southwestern Martin is typically restricted to the giant saguaros in New Mexico and Arizona. The only record of a man-made structure in this region being used by Martins is for "certain buildings at Arivaca, Ariz., more than 20 miles outside of saguaro country" (Van Rossem, 1936: 140). From one to three pairs usually nest per giant cactus, the bird's showing no tendency to concentrate in a small area (M. B. Cater, letter).

MAN-MADE SITES

The first nest boxes offered by man to birds in this country were gourds hung up by Indians to attract Martins, according to Alexander Wilson (1812, 5: 60-61): "Even the solitary Indian seems to have a particular respect for this bird. The Chactaws and Chickasaws cut off all the top branches from a sapling near their cabins, leaving the prongs a foot or two in length, on each of which they hang a gourd, or calabash, properly hollowed out for their convenience. On the banks of the Mississippi, the negroes stick up long canes, with the same species of apartment fixed to their tops, in which the Martins regularly breed. Wherever I have travelled in this country, I have seen with pleasure the hospitality of the inhabitants to this favorite bird. . . . The Purple Martin, like his half-cousin the King Bird, is the terror of Crows, Hawks, and Eagles. These he attacks whenever they make their appearance, and with such vigor and rapidity, that they instantly have recourse to flight."

Audubon (1831, 1: 117-119) gives a few more details as to the services rendered by the Martins to the Indians and the farmer. "They exhibit strong antipathies against cats, dogs, and such other quadrupeds as are likely to prove dangerous to them. They attack and chase indiscriminately every species of Hawk, Crow, or Vulture, and on this account are much patronized by the husbandman. They frequently follow and tease an Eagle until he is out of sight of the Martin's box. . . . Its notes are among the first that are heard in the morning, and are welcome to the sense of everybody. The industrious farmer rises from his bed as he hears them. The still more independent Indian is also fond of the Martin's company. He frequently hangs up a calabash on some twig near his camp, and in this cradle the bird keeps watch and sallies forth to drive off the Vulture that might otherwise commit depredations on the deer-skins or pieces of venison exposed to the air to be dried. The humble slave of the Southern States takes more pains to accommodate this favorite bird. The calabash is neatly scooped out, and attached to the flexible top of a cane, brought from the swamp, where that plant usually grows, and placed close to his hut. It is, alas! to him a mere memento of the freedom which he once enjoyed; and, at the sound of the horn which calls him to his labour, as he bids farewell to the Martin, he cannot help thinking how happy he should be, were he permitted to gambol and enjoy himself day after day, with as much liberty as that bird. Almost every country tavern has a Martin box on the upper part of its sign-board; and I have observed that the handsomer the box, the better does the inn generally prove to be. All our cities are furnished with houses for the reception of these birds."

Wilson and Audubon have often been quoted, but neither of the authors of the present paper have been able to find any other original observations on the relations between Martins and Indians.

That white settlers early offered accommodations to these birds is shown by Catesby (1731, 1: 51), who was in the Carolinas and Florida between 1712 and 1726: "They breed like Pigeons in Lockers prepared for them against Houses, and in Gourds hung on Poles for them to build in, they being of great Use about Houses and Yards for pursuing and chasing away Crows, Hawks, and other Vermin from the Poultry."

In all these early overtures to the Martin there was a strong utilitarian motive: I offer you a nesting place; you protect my meat, hides and poultry. This reciprocal relationship still holds where fowls are raised. But a vast number of Martin houses are now erected purely in the hope of the pleasure of seeing and hearing these notable birds:

Purple Martins have adopted other structures of man besides those designed for them—crevices in buildings (Roberts, 1932), under bridges, above arc lights (Bagg and Eliot, 1937). "I have observed a colony of Purple Martins nesting about the top of an old five story building in Jackson, Michigan." (A.)

"Martins were undoubtedly colonial before the coming of the White Man to North America. They could hardly, however, have been as colonial as they are today, as trees do not ordinarily have facilities to house very many pairs." (A.)

NESTING POPULATIONS IN ANN ARBOR AND BLUE ISLAND

In 1940 a census was made of Martin colonies in Ann Arbor. Twenty-two colonies with a total of 37 houses containing 761 rooms had a population of 191 pairs, an average of 5.2 pairs per house, 8.7 pairs per colony. The birds occupied 23.5 per cent of available rooms, the highest per cent of occupancy being 50, the lowest 10. The size of colonies ranged from one to 39 pairs.

In Blue Island, Illinois, a suburb of Chicago, Karl Bartel (1945, 1947) has made a census of Martins for 14 years; he has aroused considerable civic pride and emulation among the 40 or more owners of colonies. The number of colonies ranged from 29 to 40, the number of pairs from 151 to 331, averaging 7.9 pairs per colony. Eleven per cent of the boxes have been entirely filled, the largest number of pairs in any one colony being 42 (personal communication). House Sparrows and Starlings are eliminated by means of the rifle.

Milam B. Cater of Millboro, Virginia, writes that Mr. Connie Watts of Baldwin, Georgia, has 74 gourds hanging from three poles and that "each gourd has a pair of Martins each year." A colony of 250 to 300 pairs in one house was reported from Chazy, N. Y. (Hamilton, 1909).

RECOMMENDATIONS FOR MARTIN HOUSES

Houses for Martins should be set well out in the open, at least 20 feet from the nearest tree or building. They should be 20 or 30 feet above the ground.

As to size of rooms, many authors have advised too small compartments, for instance: 5 x 5 x 6 inches or 6 x 6 x 7 (Jacobs, 1909), or $4\frac{1}{2}$ x 8 x 7 (Bailey, 1928). Widmann (1905), however, recommended rooms 8 x 8 x 6 inches high with a double roof, Bagg and Eliot (1937) a 10-inch diameter for the apartment and an empty, enclosed space on top, and Bartel (1947) "triangular rooms with the entrance near the small angle," 8 x 12 x 14. The relation between room size and success of nesting is discussed on pages 645-646.

Doors should be large—2½ inches in diameter. Landing shelves should be narrow to discourage House Sparrows; besides wide ones may tempt the young Martins abroad too early. The house should be taken down after the birds leave and thoroughly cleaned and disinfected. Robert Mitchell, entomologist at the Patuxent Research Refuge, recommends a liberal dose of DDT powder in each room before the house is put up in the spring. He believes that this would not harm the birds, but would lessen infestation by parasites.

Territory and Pair Formation

The nesting period of the Purple Martin may be divided into seven stages: (1) taking up territory; (2) pair formation; (3) pre-nuptial period; (4) nest building; (5) egg laying; (6) incubation; (7) care of young. In this section the first two stages will be considered.

"The first visits to the colonies are, almost always, of very short duration, seldom lasting more than an hour. The birds alight on the house and sit there quietly for a time; the males may give a few songs and go in and out a few of the rooms. Then the group will leave the house and may not be seen again for several days or possibly weeks.

"In the Ann Arbor region the birds usually begin to settle down around the middle of April. Hitherto, every spell of bad weather has driven them from the vicinity; now bad weather drives them to the house. In the flocks which arrive early both males and females may be present, with the males usually in the majority. These birds often visit a number of houses before they settle down." (A.)

THE MALE SELECTS A NESTING TERRITORY

"Now the male, upon visiting a house, becomes much interested in the rooms; he goes inside one and may stay as long as ten minutes. He goes inside another and stays in it a while; he may try almost every room in the house and then return to the first one or fly to a nearby house.

"He soon selects a room or, rather, part of a house, for some individuals will attempt to dominate a number of adjacent rooms. In one three-story house with two rooms on each end and three on each side per story the males settled so that there was one on each story on each side, thus getting as many birds as possible into the house without bringing any into close contact.

"As new birds arrive at the colonies they attempt to enter rooms that other males have taken for their own. The result is that battles are numerous and violent. The fighting takes two forms. When an adult male sees another adult male alight on the porch in front of his room he either advances and fights the intruder or he retreats into his room. In the first case the intruder may leave at once, or the two will fly up together, each having a claw hold on the other, and flutter in the air a few seconds, then fall to earth. Usually they separate just before striking the ground, but occasionally will continue the battle on the ground for some time.

"In the second case, when the intruder follows the owner into the room, a

fight results; one or the other of the birds is usually worsted in a short time and attempts to leave. However, the victor usually has a firm claw-hold on his feet or wings and will not let him go. Rather he sits in the doorway holding his foe dangling below and struggling in vain to free himself. Such battles may last for ten minutes or more. Once a male kept another in this position for 35 minutes, pecking him violently the whole time. How long this would have lasted I cannot say, for a man walked past and frightened the birds.

"The fighting begins when the first males settle down in the colony and continues as long as new birds are arriving. However, once a male has settled upon a place he seldom trespasses on his neighbors' property and his only fights are with those that seek to trespass on his domain. The birds do not seem to get much hurt in the fighting.

"Throughout this period the male sings repeatedly, usually from the porch in front of his room and occasionally from the house top. The song is frequently heard when a male on a house sees other birds flying over, thus advertising the presence of the house to passersby." (A.)

THE FEMALE SELECTS A ROOM

"When a female arrives at an established colony, each male remains near his own room and calls loudly. If she alights on his porch, his excitement is redoubled. She seems to be indifferent to him, but peers into different rooms. She may enter a large number of rooms or only a few; one bird spent nearly the whole afternoon going between two rooms. In several instances where I timed a house-hunting female, she stayed about as long around rooms that had no males as around those that had one in attendance. The males are much more ardent in the early morning than later in the day; house hunting can go on in the afternoon with very little attention from them. When they are excited, however, they will fly out after the female and sometimes follow her to the domain of another male where they are usually promptly driven out. Finally the female seems to settle upon one place and the male that had chosen that room or the one nearest it has a mate. From start to finish the whole process seems to be more of a house hunting than a mate hunting.

"In the course of house hunting, females often encounter other females. If the house hunter enters a room already containing a female, a fight ensues. Such fights usually last only a minute or two, although one bird may hold another in the doorway as do the males. The females seem interested only in defending the room.

"A female may take several days before she definitely settles down. She will seem settled one evening and the next day begin the search all over again. Finally she will become suited, but even then she may occasionally go out on a tour of the other rooms of the house and get into fights with the owners. Such occasional expeditions may occur as late as two weeks after the bird's arrival, but they seldom result in any change of place.

"As soon as the Martins once settle in a house, it becomes their head-

quarters for the rest of the season. Here they sleep and here they seek refuge from snow and rain. On days of particularly bad weather I have seen all the birds gathered on the protected side of the house and here they spent the day. One morning I came to observe the birds when the house was covered with snow. Not a Martin was in sight. I had concluded that the birds must have left for a warmer climate when I heard a chirp and saw a single male come from his room, walk out on the snowy porch, give a few chirps, and then return to his room. The entire colony was in the house and there they remained until the weather became more agreeable." (A.)

THE PRE-NUPTIAL PERIOD

"After the birds have settled in a colony there is a period of two to three weeks before they begin to nest. They spend their time feeding, sitting about the house, and preening. Occasionally they have to eject an intruder from their domain, but generally peace prevails. The male continues to sing during this period but does not attempt copulation. If the weather is cool, a great deal of time may be required for the birds to obtain sufficient food." (A.)

SEX DISCRIMINATION

In many birds where male and female plumages are similar, sex discrimination seems to depend upon behavior and notes. But when the sexes are dimorphic, birds may discriminate on sight.

"I have often seen a male Purple Martin allow three or four females to enter his room during a morning, but when a male tried to enter there was a battle. The females had, so far as I could tell, no behavior that acted as a releaser. It seems more probable that the color difference between the sexes makes the distinction possible. The plumage of the first year male is much more like that of the female than that of the fully adult male and it was interesting to note that the adult males tolerated them. I observed a first year male that nested next door to an older male and never saw a fight between them. The first year males are, sometimes at least, belligerent toward the other males." (A.)

Nest Building

"The third period in the nesting cycle is characterized by nest building, copulation and sexual fighting." (A.) This period corresponds to Howard's (1929) Third Phase with the Reed Bunting, *Emberiza schoeniclus*, Timbergen's (1939) Fifth Stage with the Snow Bunting, *Plectrophenax nivalis*, and Nice's (1943: 170) Fourth Stage with the Song Sparrow.

BUILDING THE NEST

"In southern Michigan nest building usually begins in early May, about a month after the first birds are seen and two to three weeks after the birds have settled down at the colony. It continues until four or five days before the eggs are laid, a period of three to four weeks. It is rather difficult to say

when the nest of a Purple Martin is complete, as material is added to it irregularly even after incubation has begun. Some late-arriving individuals seem to be able to build as satisfactory a nest in a week as some of their neighbors did in three. The early builders, however, usually get their nests done in ten or twelve days and then occasionally add a few pieces of material until the eggs are laid. When the first nesting is broken up, there is a minimum of building for the second set; a few straws are added to whatever some previous tenant has left in the box and the affair is complete." (A.)

In 1938 nest building was first noted on May 2, in 1940 on May 7. In 1938 the temperature the last week of April averaged 5° F. per day above normal; building started May 2 with a mean temperature of 63° , 11° above normal. Two years later the last week of April averaged normal temperature, while the first four days of May were 10° below normal per day. May 5 was 1.4° above normal, May 6, 11° above and May 7, on which day building began, 5° above.

"On May 2, 1938 a male bird flew to the ground; after remaining quiet for about half a minute, he took a few steps and picked up a stalk of dead grass, held it in his bill for a few seconds, dropped it and flew away. A little later another male repeated the performance, but this time carried the grass to the nest box. The gathering of nesting material seems to be a contagious activity; one bird drops to the ground and several others often follow immediately. On this first morning the females also flew to the ground, but I did not see them pick up anything. Most of the males failed to complete the reaction; some dropped the material just as they were starting to fly, while others carried it as far as the porch of the house, but only a few got it inside a room.

"For the first few days the males are more active in getting material than are the females. By the time the female begins building in earnest she has selected the room she intends to occupy and she confines her attention to it. The male is not so dependable. It is not an uncommon sight to see a male carrying a thick weed stem or stick to the house and attempting to push it into his room. Since such things are nearly always carried in the center, it is often extremely difficult or impossible for the bird to force his way into the room with the twig in his bill. Each time he tries to enter, the ends of the twig catch on the sides of the doorway. After trying his own room for several minutes, he usually tries some neighboring room. Sometimes as many as eight different rooms were tried before the bird gave up and dropped the stick. If the male comes to the room with nest material and finds his mate sitting in the doorway, he is likely to take his load into one of the adjoining rooms. If this is occupied by another male, a fight follows. Several pieces may be brought at one trip. So much trouble is experienced in getting material into the rooms that each day's activity results in a litter of old stems around the base of the poles.

"Females are much better oriented in their attempts to get nest materials into the rooms. They are not so ambitious as the males in regard to the size of the things they will pick up and hence are not so often frustrated in their

attempts to get them into the room. In uncrowded houses, however, even females may sometimes carry stuff into two rooms.

"Purple Martins prefer to alight on bare ground to pick up nest material. They are always rather nervous and easily frightened when on the ground. In 1938 plant materials were obtained from a field 150 feet from the colony and the mud from the top of a dam across the Huron River 800 feet distant. Both birds would make the trip, the male following his mate.

"As the season progresses, the females become more intent on nest construction and the males lose interest. At the end of the nest-building period the males carry very little material, but spend most of their time following their mates and courting them." (A.)

COPULATION AND SEXUAL FIGHTING

"It is during the three or four week period that is occupied with nest building that sexual flights and copulation take place. When both birds of a pair are on the ground, the male may 'pounce' upon her, by suddenly flying toward her and striking her on the back. He may alight on her back if she will allow it. At the beginning she resists fiercely and flies away; he follows and they race around the colony in great circles until she alights on the house and the affair is over for the moment. These 'sexual flights' are very contagious, other males often joining in the chase.

"At this time another type of fighting begins. This usually occurs when the female has flown to the ground accompanied by her mate; some other male alights nearby and the first male attacks him and drives him away. If the male of one pair sees another male approach his mate while she is on the ground and he on the house, he will swoop down and drive the other away. This type of fighting becomes more common as copulation begins, and disappears as soon as the female will no longer copulate.

"Copulation may take place on the house or on the ground; it is usually confined to the early morning hours. The initiative is taken by the male; when the female has reached the proper physiological stage she flattens herself and the male mounts. Copulation ceases with the laying of the first egg. The male sings throughout the period but not as often as in the first and second periods." (A.)

THE NESTS

"The nests are constructed of twigs, stems of herbaceous plants, leaves from trees, and mud. In many localities feathers are also used. Mud is the most variable item; its use seems to depend upon the situation of the nest. Some Martin houses have large doors which allow the wind and rain to enter; here the Martins often build a wall of mud that protects the nest. In one house I examined there were no walls to the nest on the east and south sides, but almost all of them on the north and west side were thus protected. Widmann (1922) says that in rainy seasons more mud is used and some boxes facing west have been found to contain regular walls of mud between the entrance and the nest, the mud-wall itself weighing as much as eight ounces.

"The twigs and grass stems are placed on the floor of the box behind the

wall (if one is present) with little apparent attempt at design. At the rear or at one side, if the room is wide, is a depression in the mat in which the eggs are laid. The amount of material varies greatly, large rooms generally having bulkier nests than small ones. Some birds will fill the box to a depth of several inches, while others seem content with barely enough to cover the floor.

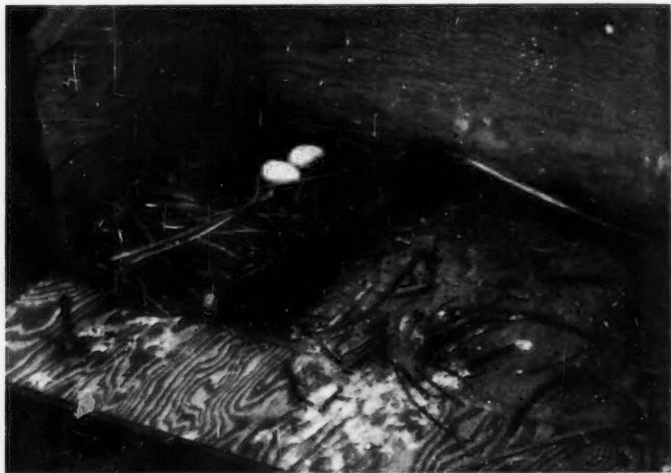


Fig. 4.—Nest of Purple Martin with two eggs

"After the main structure of the nest is completed the adults line it with green leaves. Both sexes gather leaves from small trees, apple, pear, or willow. The leaves are not worked into the nest structure, but are placed on top of the other material. They are brought while the eggs are being laid and, by the male at least, during incubation. The number carried varies among individuals; one male watched brought a leaf nearly every time he came to call his mate from the nest. A nest examined at this time shows leaves at all stages from fresh to dry.

"The function of these leaves is uncertain. Widmann (1922) writes: 'Often the precaution is taken to cover the newly-laid eggs with a fresh supply of green leaves. Besides concealing the eggs from the eyes of intruders it also serves to keep them cool.' They undoubtedly do cover the eggs during egg laying and may have some value there; as to cooling, however, this seems very unlikely to me. It seems doubtful if they would be very effective in this capacity, as no nest I have seen had more than three or four leaves that were really fresh. And why should they be carried in during late May and early June when the birds do not need a cooling system as much as a heating system?" (A.)

This matter of green leaves is discussed by Taverner (1933). The Martins at Ottawa, Canada, "alight on outermost twigs and seem to worry off individual leaves with some trouble and awkwardness. . . . At other times I have seen them carry leaves from the nest and drop them in the immediate vicinity. On a number of occasions I have marked the fluttering fall of the leaf to the ground and examined it. In every case, while still green, it was dry to brittleness . . . this leaf gathering is most active during (or confined to) the incubation period and usually ceases as soon, or shortly after, the young are hatched. The conclusions are, that the leaves are taken in to supply the needed moisture for incubation, as the poultry raiser adds moisture to his incubators. It is a well known fact that many hawks add green branches to their nests."

Jacobs (1903: 13) says that the eggs "are partly covered with bits of apple leaves which they pluck from the tops of the apple trees, or with the seed pods of the locust tree which they find on the creek bank."

"Great and especially Blue Tits [*Parus major*, *P. caeruleus*] sometimes 'decorate' their nests during incubation with small pieces of green vegetation placed round the perimeter of the nest-cup; these 'decorations' differ from the materials used for building, and include such objects as green leaf-buds, the tips of bracken and fern-fronds, and small fragments of green leaves, about one-quarter inch square, torn from low-growing plants. This behavior, the significance of which is not known, has been recorded in other birds, e.g. *Sylviidae* and *Falconiformes*." (Gibb, 1950: 512).

"The size of the base of the Martin nest is, of course, determined by the size of the room; the cup usually measures $3\frac{1}{2}$ to 4 inches in diameter. Nests weigh from 50 to 300 grams, depending largely on the presence or absence of mud. By the time the young have grown the nest has lost whatever semblance of form it ever had; mud walls are broken down and the nest material has been trampled into a dense mat on the floor." (A.)

Egg Laying

"With the beginning of laying—stage 5—the Martin colonies become much quieter. So closely do the birds stick to their own parts of the house that fights are rare. They no longer go to the ground, so the second type of fighting has ceased. Pouncing and copulation are no longer seen. The male stays close to his mate when about the house and they feed together. His songs are as frequent as before." (A.)

THE EGGS

The eggs are pure white in color and without gloss. (Mayr and Bond (1943) classify the Swallows according to their method of nesting: (1) in natural hollows—probably the most primitive; (2) new nesting holes excavated; (3) mud nests constructed. Swallows in the first and second groups lay white eggs, while some in the third group lay white eggs, others spotted eggs.) Jacobs (1903) gives the average measurements of 62 eggs in Pennsylvania as 24.3×17.1 mm.; Bent (1942) of 50 eggs without locality as 24.5×17.5 .

"As to weight, 65 fresh eggs ranged from 3.4 to 4.6 grams, the average being 4.1 grams. In four sets that were weighed as laid, the first egg was always the lightest and usually each thereafter weighed a little more than the one before it; in no case did it weigh less. The difference in weight from the first egg to the last was 0.2 grams in one set, 0.5 in two sets, and 0.6 in one set.

"In 84 sets in the Ann Arbor region, I found seven eggs in 1 per cent of the nests, six eggs in 19 per cent, five eggs in 54 per cent, four eggs in 25 per cent and three eggs in 1 per cent, an average of 4.9 per nest. Widmann (1922) reported the same average in 45 sets in Missouri. In second sets I have never found any number other than four. All four egg clutches were either second sets or were laid by the mate of a first year male, presumably a first year female. Eggs are laid early in the morning on successive days. In one instance when the temperature turned much cooler than normal, a late-nesting bird skipped a day between the second and third egg of her three-egg set." (A.)

In 1938 the first set at the George Reserve was complete on June 4, in 1940 on June 9. Each of these contained five eggs.

Representative egg dates are given by Bent (1942: 508): Florida, March 26 to May 19; Texas, April 30 to June 2; New Jersey, May 31 to June 1; Wisconsin, May 18 to July 19; and by Forbush (1929: 138): South Carolina, May 2 to 23; Massachusetts, May 30 to June 23; Maine, June 5 to July 4.

NUMBER OF BROODS

Audubon's cheery statement in 1831 that the Purple Martin in Louisiana "frequently raises three broods whilst with us" has made a deep impression on American ornithology. Nearly a hundred years later Widmann (1922) deplored our lack of knowledge of "our commonest birds." "For instance, do we not find in some of our best works that the Martin raises two broods or three broods in the Southern States?" "The Martin does not commence nesting in Louisiana before April, although the first arrives in February. The time required for a successful rearing of a brood of Martins does not vary much from ten weeks." Nevertheless, "our best works" continued to trust Audubon, as witness Forbush (1929) and Bent (1942: 492, 494) to mention only two. According to Baerg (1931: 103), "There are probably two broods in Arkansas."

In 1910 Wayne had stated that only one brood was raised in South Carolina; Sprunt says the same is true in North Carolina (Bent, 1942: 492). Letters of inquiry to southern observers elicited three answers. From Arkansas: "I do not hesitate to admit having no evidence that martins rear two broods in Arkansas. In fact, circumstantial evidence would indicate that they rear but one," (W. J. Baerg). From Pensacola, Fla.: "It is my very definite opinion that Martins are not two-brooded in the South. I base this opinion upon 35 years' observation in this region and several years before that in South Carolina. Young Martins are in first flight late in June, and all the birds have deserted their nesting areas by the middle of July and take up residence in the marshes until they are ready to migrate. A second brood

could not be on the wing before the middle of August (or later), and I have never seen anything like that." (Francis M. Weston)

And finally from Baton Rouge, Louisiana: "I can say definitely that there is absolutely no evidence of the species raising a second brood. Sometimes I have had new pairs come to the boxes late in the season and raise a brood after other pairs were through with theirs. Had the birds not been banded, one might have supposed that these late nesters constituted second broods." (George H. Lowery, Jr.).

Let us hope that writers will be more discriminating in what they copy from the authorities.

RE-NESTING

"The Purple Martin normally lays one set of eggs each year. If this set is destroyed or fails to hatch, the bird lays again. I have full data on only one such instance: the female began to lay ten days after the destruction of her first set.

"In late July 1940 many adults lost their young about a week before these should have left the nest. None of these made another attempt as far as I could ascertain. The season of 1940 was unusually late, so that might have been a factor in the failure of these birds to make a second attempt." (A.)

When Jacob's colony at the end of June 1902 lost more than half the young that were nearly ready to fly, the adults did not lay again (1903: 20). The next year after 80 newly-hatched young succumbed in mid-June, the parents re-nested (1909: 41).

Incubation

"The female incubates about 70 per cent of the day and the male guards the nest during her absences. Song is reduced. The male no longer follows his mate about. Few, if any, fights occur." (A.)

LENGTH OF INCUBATION

"Eggs were marked as laid and always hatched in the same succession. In 1938, three eggs of one set hatched in 16 days and the fourth in 17. In 1940, 16 eggs hatched in 15 days, 12 in 16 days, 2 in 17 and 3 in 19 days. This last case may have been due to a delay in the start of incubation." (A.)

Widmann (1922: 6) writes: "The ordinary time seems to be fifteen or sixteen days. Early broods take longer, late broods a shorter time," but in the present study the 17- and 19-day incubation periods came late in the season. As with the two- to three-brood myth, careless statements as to incubation period "12 to 20 days" appear again and again—Forbush (1929), Roberts (1932), Oberholser (1938), among others. Sprunt (Bent, 1942: 494) is clearly in error when he says "probably the normal period is 12 or 13 days."

"Incubation usually starts on the day the last egg is laid, but since the eggs often hatch on different days, some development must take place earlier. The adults usually spend the night in the room with the eggs and thus raise the temperature to some degree. On very hot days the temperature inside the house often goes above 90° F. and this would result in some development." (A.)

PERCENTAGE OF TIME THE EGGS WERE COVERED

Three nests in 1940 were watched for three to four hours a day from the beginning of incubation to near hatching. Results are shown in figure 5.

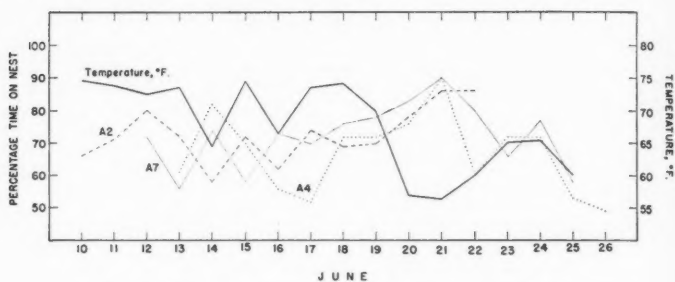


Fig. 5.—Percentage of time spent on the eggs by three females

Of the total time observed, A2 incubated 70 per cent, A4 67 per cent and A7, 71 per cent. Daily variations ranged from 58 to 86 per cent for A2, 49 to 90 per cent for A4, and 56 to 90 per cent for A7. During most of the time temperatures were about normal, averaging 69.6°F ., but low temperatures from the 20th to 22nd of June, averaging 58° or 11° below normal were accompanied by an increase in time spent on the nest, averaging 79, 89 and 75 per cent of the time (81 per cent for all three), in contrast to the average of 69 per cent for the whole period with average temperature of 67.6° . On the 21st the birds stayed on the nest for over an hour, one of them as long as 75 minutes.

This increase of time on the nest in response to low temperature was clearly shown by a European Barn Swallow, *Hirundo rustica* (De Braey, 1946; Nice, 1947) that spent 74 per cent of the day on the nest with a mean temperature of 14.8°C . and 66.5 per cent with a temperature of 21.7°C . The relationship between incubation rhythm and temperature in a number of species has been discussed by Nice and Thomas (1948) in their study of the Carolina Wren, *Thryothorus ludovicianus*.

DURATION OF ATTENTIVE PERIODS

"In order to analyze the periods of time spent on the eggs, these periods were divided into groups of four minutes duration and all records falling within the group counted together. The percentage of each group in total time of incubation is shown for the three nests studied in figure 6." (A.)

The majority of incubation periods lasted between 4 and 15 minutes, but a few much longer, especially in the cool spell which accounted for all the periods over 30 minutes. Females A2 and A4 showed similar rhythms, while A7 spent longer periods on the nest.

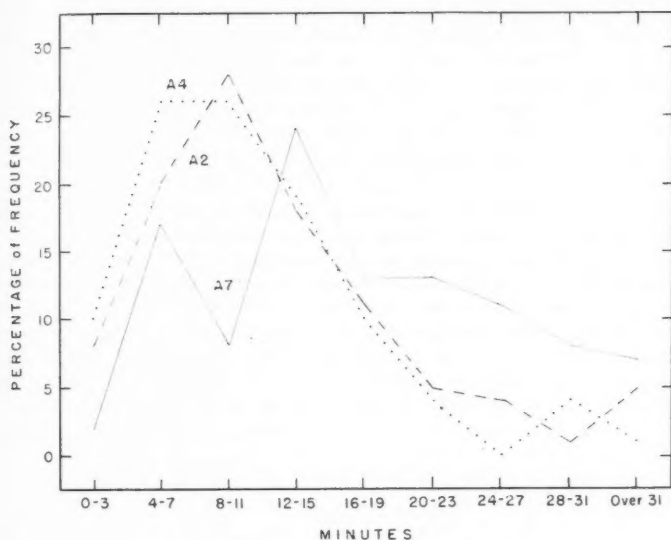


Fig. 6.—Percentage of frequency of attentive periods

DURATION OF INATTENTIVE PERIODS

"The frequency of inattentive periods of different lengths is shown in figure 7, where two minutes is the interval used. With A2 and A4 more than 90 per cent of the intervals were under 10 minutes, 5 and 6 minutes being the most common length. With A7 only 69 per cent of the intervals were under ten minutes, while the longest lasted 35 minutes. Her most frequent intervals were 5 to 6 and 11 to 12 minutes." (A.)

From June 10 to 16, 1927 records of six complete days of incubation of a female Purple Martin were taken with potentiometer by Kendeigh (in press). Percentages of daylight hours spent on the nest were 67.6 on June 10 at a mean temperature of 70° F., 80.3 the next day at 65°, and averaged 77.9 on the 12th, 14th, 15th and 16th with mean temperatures of 57°. The average percentage for the six days was 76.7, the average temperature 60.5°. The number of attentive periods per day were 24, 20, 15, 17, 25, 30 respectively, averaging 21.8. Their average length in minutes was 24.6, 34.6, 45.9, 35.4, 28.7, 22.8, giving an over-all average of 32. Average duration of inattentive periods was 11.3, 8.1, 13.1, 9.5, 8.5, 5.1, an over-all average of 9.3. The two coolest days were June 12 and 16, with means of 56°. On the 12th there were 15 attentive periods averaging 45.9 minutes, and 16 inattentive periods averaging 13.1 minutes, the longest in any day. On the 16th there were 30 attentive periods averaging 22.8 minutes, 31 inattentive, averaging 5.1 minutes,

the shortest of any day. So this bird responded to cool weather in different ways, on one day decreasing the number and increasing the length of both attentive and inattentive periods, on the other, doubling the number and decreasing their length. Yet the percentage of time on the nest was higher than when the temperature was 70° (67.6), for it reached 76.7% on the 12th, 81.2% on the 16th. The length of day from the first leaving of the nest till settling down for the night varied from 14 hours to 15 hours 37 minutes; no data are given as to sky conditions in the morning and evening.

One of the swallows studied in Tanganyika showed a somewhat similar rhythm, but with another, periods were very much shorter. With the Rough-wing Bank Martin, *Psalidoprocne holomelaena massaica*, from 6 to 20 per cent of the spells on the nest were shorter than 8 minutes, while from 28 to 62 per cent were longer than 15 minutes. In three nests 80 per cent of the periods off the nest lasted more than 11 minutes, but in two nests this was true of less than 45 per cent; (Moreau, 1940a: 239, 240) this graph shows considerable similarity to our figure 7. With the Wire-tailed Swallow, *Hirundo s. smithii*, "About 70 per cent of the spells 'on' lasted 2-7 minutes and 70 per cent of the intervals 'off' 2-5 minutes. (Moreau, 1939a: 125)

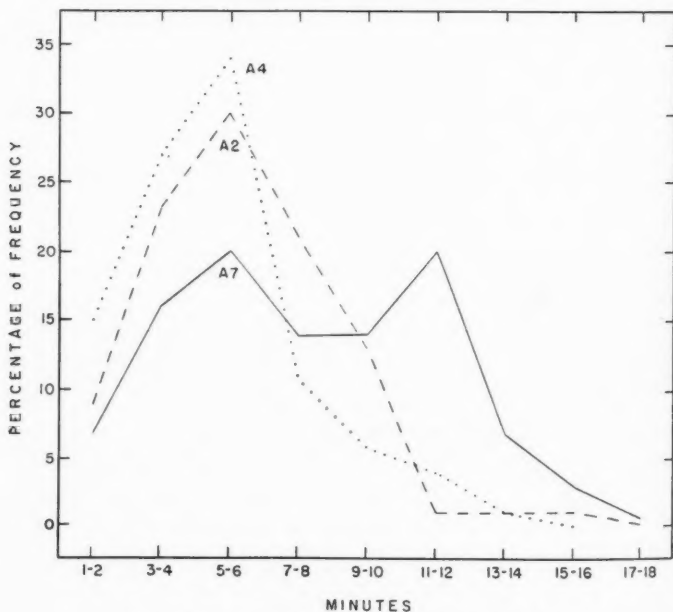


Fig. 7.—Percentage of frequency of inattentive periods

Personally, instead of these graphs showing frequency, I prefer the method used by Nice and Thomas (1948: 145) which gives number of periods on and off, their range in minutes and average length. Unfortunately this is not possible with the Martins, since the original data are not available. (M.M.N.)

THE ROLE OF THE MALE

While the female incubates, the male calls her from the nest and watches the nest during her absence. Song is reduced and no fighting occurs. Some people assert that the male assists in incubation (Bent, 1942: "Both sexes incubate the eggs," p. 492, but "Incubation apparently is performed by the female only," p. 494). The fact that he has no brood patch is good evidence to the contrary. The male seems never to have been seen feeding his mate.

"The fact that during incubation the male enters the room and remains there some minutes while his mate is absent is no proof that he is incubating. He also went into the room for short periods before there were any eggs, even before there was a nest, and before he had a mate. One male observed in 1938 spent only 4 minutes of a two hour period in the box; another spent 7, 14 and 16 minutes in the room, every time but one entering as soon as his mate departed and remaining until her return. The three males watched in 1940 differed in their behavior. One would enter the room, whereupon his mate would leave; after remaining a minute or two he came out and spent the rest of the time until his mate's return upon the porch of the house, but if she stayed away too long, he did not wait. The second bird guarded, sitting just inside the room with his head in the doorway. The third male stayed longer inside the room, from 12 to 40 per cent of the time his mate was away." (A.)

COMPARISON WITH OTHER SWALLOWS

There are dependable data on length of incubation for 14 species of Swallows, 7 in the North Temperate Zone, 7 in the Tropics.

In five species male and female regularly share incubation. In seven species the female usually takes all responsibility, although with the Barn (Smith, 1937, Morcau, R. E. and W. M., 1939b, Niethammer, 1937, Witherby, 1938) and Tree Swallows (Cash, 1933, Weydemeyer, 1934) the males occasionally assist. A very interesting case is reported by Kuerzi (1941: 27) of the only instance of a male Tree Swallow incubating in his colony: "The female of this pair died of a fungus mold disease . . . three days after incubation had begun, and the male took over incubation; on the 15th day all five eggs hatched and were successfully fledged."

In the north, incubation lasts 14-16 days in the six small species, 15-16 in the Martin. Might this slightly longer period be correlated with its much greater size, the Martin weighing almost three and four times as much as any of the others? In the Tropics incubation lasts 14 days with the Wire-tailed Swallow, 15 with the Blue-and-White Swallow, and 16 to 20 with the five other species. In general, incubation in the Tropics is prolonged in comparison with the North Temperate Zone.

TABLE 4.—Data on nest behavior of fourteen species of swallows (parentheses = occasionally)

Species	Region	Weight ¹	Sex which incubates	Number of eggs	Length of incubation	Length of fledging	Number of broods
Purple Martin	No. Am.	54.7	♀	4-6	15-16	28-35	1
<i>Progne subis</i>							
Tree Swallow ^{3, 4}	No. Am.	21.3	♀ (♂)	4-6	14-15 ²	16-24	1
<i>Iridoprocne bicolor</i>							
Violet Green Swallow ⁵	No. Am.	16		4-6	15	23-24	1
<i>Tachycineta thalassina</i>							
Bank Swallow ^{6, 7, 8}	No. Am.	14.6	♂ & ♀	4-5	14-16	18-22	2
<i>Riparia r. riparia</i>	Europe						
Barn Swallow ^{7, 8, 9, 10}	No. Am.	19	♀ (♂)	4-5	14-15	20-24	2
<i>Hirundo rustica</i>	Europe						
House Martin ^{7, 8}	Europe	16	♂ & ♀	4-5	14-15	19-22	2
<i>Delichon urbica</i>	Europe		♀	4-5	14	25-26	1
Rock Martin ⁷							
<i>Riparia rupetris</i>							
Red-throated	Africa	14?	♂ & ♀	2-3	17	25-28	
Rock Martin ^{13, 14}							
<i>Ptyonoprocne rufigula</i>							
Roughwing Bank	Africa	10	♀	2	18-19	25-27	2
Martin ^{12, 13, 14}							
<i>Psalidoprocne holomelana</i>							
<i>massaica</i>							
Stripe-breasted	Africa	14?	♂ & ♀	3	16	18	
Swallow ^{13, 14}							
<i>Hirundo abyssinica</i>							
Wire-tailed	Africa	13	♀	3	14	18-21	3
Swallow ^{11, 13, 14}							
<i>Hirundo s. smithii</i>							
Pacific Swallow ^{15, 16}	New Guinea	16.5		2-3	19-20	21-23	2
<i>Hirundo tahitica</i>	Central America						
Salvin's Rough-winged Swallow ¹⁷			♀	4-5	16-18	20-21	1
<i>Stelgidopteryx ruficollis</i>							
<i>fulvipennis</i>							
Blue-and-White Swallow ¹⁷	Central America		♂ & ♀	3	15	26-27	2
<i>Pygochelidon c. cyanoleuca</i>							

¹ Weights of North American species supplied by Dr. J. Van Tyne from specimens in the Museum of Zoology, University of Michigan; of African species by Mr. R. E. Moreau; those of European species found in Niethammer, 1937, of Pacific Swallow in Heinroth, 1922. ² Austin and Low and Kuerzi give 13-16 days incubation for the Tree Swallow, but calculated the period from the laying of the last egg to the hatching of the first, even although eggs often hatched over a period of 2 days. ³ Austin and Low, 1932. ⁴ Kuerzi, 1941. ⁵ Edson, 1943. ⁶ Stoner, 1936. ⁷ Niethammer, 1937. ⁸ Withersby et al., 1938. ⁹ De Braey, 1946. ¹⁰ Smith, 1937. ¹¹ Moreau, 1939a. ¹² Moreau, 1940a. ¹³ Moreau, 1940b. ¹⁴ Moreau, 1947. ¹⁵ Meyer, 1934. ¹⁶ Nice, 1935. ¹⁷ Skutch, 1945.

Birds nesting in protected places typically have longer incubation periods than birds nesting in the open. Thus Hirundinidae in the North Temperate Zone incubate 14 to 16 days, while Icteridae, Mimidae, Parulidae and Fringillidae incubate from 11 to 13 days (Nice, 1943: 70).

As to "courtship feeding," Lack (1940: 176) stated it was "apparently absent" in the Hirundinidae, but Nice (1941) cited two instances where it had been occasionally seen in the Tree Swallow (Cash, 1933; Weydemeyer, 1934). It has also been rarely recorded in the European Barn Swallow, *Hirundo r. rustica*, and House Martin (Niethammer, 1937) but apparently not in any other Swallow.

In regard to percentage of daylight hours that eggs are covered, data are given in table 5 on five species where the female alone incubates and four species where both parents do so.

TABLE 5.—Percentage of daylight hours the eggs are covered

INCUBATION BY FEMALE ONLY	Nests	Flora	Range	Average	Author
North Temperate Zone					
Purple Martin	{1 3	91 50	68-81 67-71	76.7 69	Kendeigh (in press) R. W. Allen
Barn Swallow	{1 5	65 317	66.5-74 63-77	71.2 70?	De Braey, '46 Purchon et al., '48
Tropical Zone					
Wire-tailed Swallow	3	200?	43-66	55	Moreau, '39a
Roughwing Bank Martin	5	300?	31-66	49	Moreau, '40a
Salvin's Roughwing	1	6	55.9-62.9	60	Skutch, letter
INCUBATION BY MALE AND FEMALE					
North Temperate Zone					
House Martin	1	10.3	95-100	97	Moreau, R. E. & W. M., '39b
Bank Swallow	1	9.5	90+	90+	Moreau, R. E. & W. M., '39a
Tropical Zone					
Red-throated Rock Martin	7		50-90	70	Moreau, '39b
Blue-and-White Swallow	1	13	86-93.7	90	Skutch, letter

In the first category the two temperate zone species average from 69 to 77 per cent. The three tropical species show a lower percentage—49 to 55 in Moreau's thorough studies, 60 in Skutch's brief one. The average for the seven studies is 64.4, if the figure for each study is given equal value.

The four species where both parents incubate show a remarkably higher percentage (over 90) in the temperate zone species, and 70 to 90 in the tropical species, an average of 87 for all. Corresponding data on 19 nests of eight other passerine species in the North Temperate Zone, when the female alone incubated, range from 63 to 85 per cent, with a median of 76 (Nice, 1943: 221). With two tropical species the percentage was 60 and 67. We do not have enough information to judge whether this higher percentage of time spent on the nest with both parents incubating shortens the incubation period.

The Young in the Nest

"This is the busiest part of the breeding season. The parents pay little attention to each other, and as the nestlings grow they become increasingly absorbed in keeping them fed. There is little song and no fighting. When the young are about 12 days old, the parents give up sleeping in the box and begin roosting in trees." (A.)

DEVELOPMENT OF THE YOUNG

"One young Purple Martin weighed 2.8 grams directly after hatching. Individuals hatched early in the morning will weigh as much as 4 grams by nightfall. The little birds gain rapidly until 12 days of age, when they weigh from 42 to 47 grams. After this they gain less rapidly until about the 20th day when they weigh between 55 and 60 grams. They then begin to lose weight, and when they leave the nest at about the 28th day, they weigh between 47 and 52 grams." (A.) Eight adult males from Michigan, Wisconsin and Ohio in the University of Michigan Museum of Zoology ranged in weight from 49.5 to 64 grams, averaging 58; seven females from Michigan ranged from 51 to 56.5 grams, averaging 54.2 grams.

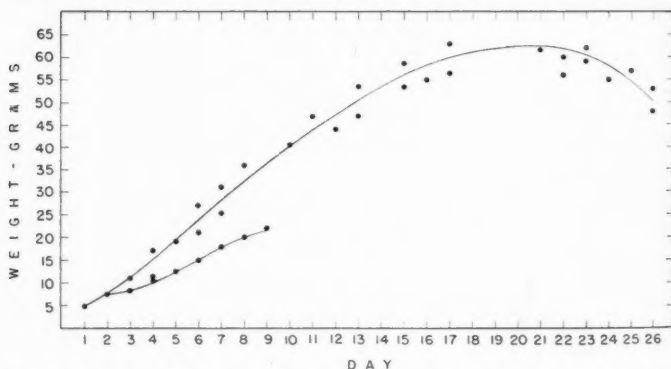


Fig. 8.—Growth curves of two sets of young birds. The upper line shows the growth of eleven normal young; the lower line depicts that of four parasitized birds

"Most newly hatched Purple Martins I have observed were entirely devoid of natal down. Two individuals possessed a few filaments: one had four grey filaments 4 mm. in length on the occipital region, the other had two of the same length on the spinal tract. Both lost this down on the first or second day of nest life. At hatching the rectrices and remiges can be seen beneath the skin and their tips protrude about $\frac{1}{2}$ mm. The inside of the mouth is a pale yellow. The line that marks the eye slit can be seen high up on the eyeball. A small egg tooth is present.

"The young bird rests on its large abdomen with the head curled around

much in the same position as in the egg. Legs and wings dangle at the sides and are not used for support except when the bird begs for food. Only when a sound or touch stimulates it to beg for food does the little bird wake from its sleep. Then it weakly lifts its head and raises its body by means of its wings and legs and utters a faint *cheep*. This reaction is not as easily obtained from young Martins as from many passerines; it is difficult to get more than one reaction from a young bird unless it is fed.

"The second day the birds are little changed except for increase in weight, but the dorsal feather tract can be seen through the skin. From the third to the sixth day the bird increases in weight and becomes more active in righting itself when overturned. The eye slit deepens and on the sixth day the eye can be opened, although it is usually kept closed. The feather tracts gradually appear under the skin and become darker in color. From the seventh to eleventh day the bird continues its increase in weight, but still remains inactive. The feeding reaction can be obtained most easily when the birds are about eight days old. About the ninth day the eyes are kept open to some extent and by the eleventh day most of the time. The skin which was at first flesh colored becomes dull blue because of the feathers developing beneath it; as yet the feathers have not begun to emerge from the skin.

"From the twelfth to the twentieth day the bird grows a large part of its coat of feathers. The rectrices and remiges are the first to begin this rapid growth. The sixth primary increases from 4 to 70 mm. during this period. Rectrices and remiges start losing their sheaths about the fourteenth day and on the twentieth only a small sheath remains around the bases of these feathers. On the fourteenth and fifteenth days the rest of the feather tracts begin their rapid growth and by the twentieth day this is largely completed.

"The first appearance of fear reactions occurs on the fourteenth or fifteenth day. At this time the birds will crowd to the back of the room and remain very quiet when in danger. If picked up they will struggle and peck at the hand that holds them. Even after being placed on the ground they will remain perfectly quiet until disturbed again, when they may try to escape by running over the ground. As they grow older they lose the tendency to remain quiet and will attempt to find a place to hide when set down. Later they will not stay in the room when frightened, but will attempt to fly long before they are capable of doing so successfully. On the fifteenth or sixteenth day they will return to the room if placed on the porch in front of it.

"From the twenty-first to twenty-eighth days the birds lose weight while completing the growth of their flight feathers. It is essential for them to be able to fly when they leave the nest and to be able to return to the same spot where their parents fed them, as the adult birds will not feed their young on the ground." (A.)

LENGTH OF FLEDGING

The young spend from 27 to 35 days in the nest, usually about 28. Forbush (1929: 141) states that they "sometimes remain in the nest for six weeks." Widmann (1922: 7) writes, "When four weeks old the pinions are

far enough advanced to carry the young bird a short distance in the air and the parents decide that the time has come when the offspring should leave the nursery." Yet on p. 10, "The young Martins do not leave their box until they are six weeks old." Possibly he meant *permanently*, for after the young have made one or more successful flights they return to the nest for considerable periods. Widmann (1922: 8) says the parents usually bring some or all of the fledged young back to spend the night, some even for 10 nights.

"When the young birds are near the time of leaving the nest they will attempt flight if frightened. They normally leave at the age of 28 days. The parents have a great deal of trouble getting some of the young birds going; but if a youngster can be lured out on the porch his parents will crowd him off into the air where he has no choice but to fly." (A.)

All swallows have long fledging periods, as is shown in table 4, 18 to 26 days being characteristic for many species. The Martin has the longest period of any swallow in the North Temperate Zone, perhaps correlated with its greater size. Three of the tropical species, although much smaller, have comparable fledging periods. A long fledging period is essential for swallows for they need to have their long wings fully grown before leaving the nest.

BROODING

"For the first few days after the eggs hatch, the female broods the young about the same amount of time as she spent incubating the eggs. A2 brooded the young on the day of hatching for 71 per cent of a 200-minute period. At this time the female almost never visits the nest without brooding the young. The male feeds the young and may occasionally remain in the nest for 4 or 5 minutes. The percentage of time spent in brooding falls to about 50 when the young are five days old, and usually stops altogether on the ninth or tenth day. In one case the parents did not spend the night in the room with nine day young when the temperature was 78° F., but two nights later when it fell to 65° they did remain.

"Moreau found that with both *Hirundo smithii* and *Psilidoprocne* young were brooded for the first days after hatching from 40 to 60 per cent of the time, and that brooding stopped after nine days (1939a, 1940). Stoner (1936) writes, 'During the first few days of its life the young bank swallow is brooded almost constantly by one or the other parent.' Austin and Low (1932), on the contrary, say of the Tree Swallow, 'Apparently the adults brood the young but very little, and spend most of the hours of daylight during this stage on the wing catching food.'" (A.)

SANITATION

"Fecal pellets are removed by both parents and are carried away from the nest and dropped from 20 to 100 feet away. After the young get to be about 20 days of age, they void the pellets out of the nest." (A.)

FEEDING

"Both parents feed the young, the female usually a little more than the male. Usually they feed every few minutes for eight or ten minutes, then

cease feeding for a similar period. A female with large young may bring food 5, 20 or even 30 times an hour." (A.) At a colony in Ontario, "Numerous counts at different times of the day during the first two weeks of July, 1917, showed that, with remarkable regularity, a parent arrived with food every thirty seconds. This year nine pairs occupied the house, and assuming that each pair had four young, and that they were fed in turn, then each nestling was fed every eighteen minutes." (Macnamara, 1917: 52) Each pair was calculated to have fed 200 times a day.

A remarkable observation on the feeding of Martins was made by Widmann (1884, reprinted 1922); on June 24, 1884 he counted the number of trips made from 4 a.m. to 8 p.m. by the 16 pairs at his house. It is a pity that he did not give more details, both as to age and number of young, and as to his technique. He must have had assistance in such an ambitious undertaking. Widmann was a careful observer and his results are consistent.

"The Martins began hunting at 4:15, but no food was brought until 4:30," (1922: 9). The number of visits from 5 to 6 was 118, during the next hour 171, for the next six hours they totalled 202, 232, 276, 255, 217, 250; from 1:00 to 3:00 they dropped to 132 and 119 during a light rain; they reached their maximum—459—between 3:00 and 4:00, while the last four hours came to 224, 166, 195 and 177.

"As a rule the older the birds in the nest the oftener they are fed, and from the size of the insect which the parents bring the age of the young may be judged. The youngest birds are fed at longer intervals with crushed insects, mostly small beetles, from the craw. About a fortnight old they are fed from the bill with soft insects of the size of large flies, but insects with stings, such as bees and wasps, are never brought. When four weeks old, large dragonflies, grasshoppers and butterflies make their principal food." (1922: 9-10)

Widmann's table gives weather conditions for each hour of the day (temperature 74°-92° F.) and the number of trips to each box per hour, as well as the total number of visits to each box by male and female. He arranged the boxes in order of total number of trips—from 312 at No. 7 to 90 at No. 6. In the text he gives the approximate age of the young in five cases, the others being "of all ages." As to the number of young, Box 7 had four nestlings, Box 16 two, "while most of the other boxes have three." A rearrangement of his results by ages is shown in table 6, where details are given for the 5 boxes where the age was reported, while the 11 other boxes are summarized.

It seems evident that both age and number of young influence the rate of feeding, although we are hampered by lack of exact information on both these points. Assuming three young to each of the boxes but Nos. 7 and 16, and counting the day as lasting 15.5 hours, we find that week-old young received 30 meals per bird per day, or 1.9 an hour, four-week young 78 meals or 5 per hour, and five-week young 96 meals, 6.2 per hour.

The average of all 16 boxes is 4.4 times per hour per bird for "all ages." The average age of the birds in the first five boxes was four weeks and the

average number of meals per hour 4.9. As to the number of meals per hour per brood, averages ranged from 5.8 with week-old young to 20 with 4 four-week young. The average for the whole colony was 13.2 feedings per hour.

TABLE 6.—All day feeding of martins at St. Louis, Missouri

	Five Boxes					11 Total Other Boxes	All Boxes	
Box number	6	7	16	12	17	"All ages"		
Age in weeks	1	4	5	5	5			
Number of Young	3?	4	2	3?	3?	15?	33?	48?
Male fed	33	119	61	164	140	517	937	1434
Female fed	57	193	131	120	140	641	1182	1823
Both fed	90	312	192	284	280	1158	2119	3277
Meals per brood per hour	5.8	20	12.4	18.3	18.1	14.9	12.4	13.2
Total meals per young	30?	78	96	95?	93?	77?	64.2?	66?
Hourly meals per young	1.9?	5	6.2	6.1?	6?	4.9?	4.1?	4.4?

The number of meals actually brought to individual boxes during one full hour differed widely. In No. 6 with week-old young it ranged from 2 (the lowest count of all) to 10. In No. 7 with 4 four-week young it ranged from 7 to 41—the highest count at any box. At No. 16 with 2 five-week young it ranged from 5 to 24.

At 11 boxes the females outdid the males, at two they brought an equal number of meals, at three the males brought more. For the 16 boxes the females made 55.6 per cent of the trips. Interestingly enough, each pair averaged 200 trips on this day, the same number Macnamara calculated for his Martins.

In table XXV (Nice, 1943: 235) the hourly rate of feeding during nesting life is summarized from studies of ten passerine species. The Ovenbird, *Sciurus aurocapillus*, brings very large meals at long intervals, averaging 0.9 trips per hour, and so does the Robin, *Turdus migratorius*, with an average of 1.9 trips per hour per nestling. Seven of the other species range from 3.1 to 5.5, averaging 4.3 trips. This is almost the same as the average of Widmann's Purple Martins, assuming that 48 young were involved.

Nesting Success

Purple Martins, dependent as they are on nesting cavities prepared by some agency other than themselves, and on flying insects as their sole source of food, are more vulnerable in their reproductive attempts than many less specialized birds.

NESTING SUCCESS AT THE GEORGE RESERVE

"It would appear that Purple Martins with their nests secure in man-made homes high above the ground would have a comparatively safe existence and would be able to raise a high percentage of their young, at least to the flying stage. This, however, was not true in my experience. Table 7 shows the losses of eggs and young birds for three years at the George Reserve.

TABLE 7.—Nesting success of purple martins at the George Reserve

	1938	1939	1940	Three Years	
				Numbers	Per cent
Number of pairs	13	4	12	29	
Eggs laid	67	19	57	143	100
Hatched	62	17	40	119	83.2
Infertile	1	2	11	14	9.8
Fell out	4	0	0	4	2.8
Disappeared	0	0	6	6	4.2
Young fell out	17	5	7	29	20.3
Died in house	4	4	17	25	17.5
Disappeared	2	2	5	10	6.9
Fledged	39	6	10	55	38.5
Percentage of success	58.2	31.6	17.5		38.5

"The season of 1938 was the most successful. In that year the only important cause of loss came from young birds falling from the nest during a hot spell just before they were able to fly. In 1939 fewer birds were under observation and of these some fell from the box and others were killed by *Protocalliphora* [= *Apaulina*, see Hall, 1947] larvae. The year 1940, however, was a disastrous one for the Martins. The spring was cold and wet and breeding was delayed about two weeks later than usual. It was cool just after many of the young hatched and the adults had difficulty getting enough food. At the same time many of the young were suffering from a heavy infestation of calliphorid larvae and many of them perished. Just before the surviving young were ready to leave the nest, there came a hot spell with mean temperatures of 82° to 86° F. for a week; some of the nestlings left prematurely and were lost." (A.)

NESTING SUCCESS OF MARTINS IN THREE STUDIES

Reproductive efficiency of Purple Martins in studies in three different states is summarized in table 8.

The Michigan birds suffered from cold weather, hot weather, and a heavy infestation of *Apaulina*. Hot weather just before fledging in 1938, seems to have brought about a loss of 17 birds, over a fourth of the young hatched. Cold weather in the spring of 1940 may have been responsible for the large incidence (20 per cent) of infertile eggs that season. It also delayed nesting,

a condition that favored the Apaulina. Cold weather in early July brought a shortage of food making the nestlings very vulnerable to the attacks of these blood-sucking flies. Thirteen of the young (32 per cent) apparently succumbed to them this year.

TABLE 8.—Nesting success of martins in three studies

Location	Years	Nests	Eggs		Hatched		Fledged		Fledged per pair
			Laid	per nest	No.	%	No.	%	
Michigan	3	29	143	4.9	119	83.2	55	38.5	1.9
Missouri	1	45	220	4.9	128	58.2	110	50.0	2.4
Pennsylvania	7	294	1380?	4.7?	1100?	80.0?	850?	61.6?	2.9?
Totals and Averages		368	1743?	4.8?	1347?	77.2?	1015?	58.2?	2.8?

Widmann (1922: 1) gives figures for only one year; hatching success was poor, only 58 per cent, but few young were lost, 86 per cent of those hatched being fledged. In Michigan this was true of only 47 per cent. On page 6, Widmann mentions "the remarkably large number of addled eggs, reaching as high as 20 to 25 per cent." In another connection Widmann (Barrows, 1889: 193) writes that on an average only two young per nest were successfully reared.

Jacobs gives information on his birds from 1896 to 1902. Unfortunately his data were not very carefully compiled or reported. The one entirely reliable figure is that of the number of pairs nesting—294 (1903: 8-10). For the first two years he gives definite numbers of young raised, but with the growth of his colony from 5 to 72 pairs, his records become estimates. Each year he took a census of the nests in early June (May 28 in 1902), but at this time some of the sets were incomplete. He counted the young by the number of "young heads protruding from the various nesting rooms." He estimates that "about" 1150 eggs were laid and 850 young brought to maturity (1903: 14). But this would give an average of only 3.9 eggs for the 294 sets, plainly too low a figure. On page 13 he discusses the number of eggs laid per set, and although the information is incomplete, his figures show a regular annual increase from the start when most of the breeders were first-year birds: a yearly average of 3.6, 3.8, 4.2, 4.5, 4.7, 5, 5, an average of 4.7 eggs per set for the 7 years, only slightly less than the average in Michigan and Missouri. If 1380 eggs (294 x 4.7) were laid and 850 young fledged, the percentage of success was 62, which corresponds well with the average for 14 hole-nesting species in table 9. Hatching success seems to have been good, some 80 per cent. During only two seasons was there much loss of young. In 1901 25 of 225 young were killed by excessive heat; in 1902, of 300 young that hatched, "one half died of starvation about the time they were ready to leave the nests." (1903: 10)

It is unfortunate that we do not have more and better data on the success of Purple Martin nesting. The only detailed information comes from the present study which involved few birds and they appear to have suffered unusually heavy losses. The one year in Missouri was only moderately successful. The Pennsylvania records are only approximations.

SUCCESS OF HOLE-NESTING SPECIES

The reproductive efficiency, i.e., the percentage of eggs that develop into fledged young, of passerines building open nests has been found to average between 40 and 48 per cent in the North Temperate Zone (Nice, 1937: 143). The reproductive efficiency of hole-nesting species is typically higher. Information on the success of 14 hole-nesting species in North America and Europe is given in Table 9.

The 32 studies cited in the table were carried on from one to 21 years. From 11 to 5000 nests were involved, and from 74 to 45,456 eggs. I am much indebted to four ornithologists who most kindly sent me unpublished data: Mr. Chapman for his Tree Swallows, Mr. Gibb for his titmice, Mr. Kluijver for his Great Tits and Mrs. Laskey for her Bluebirds.

Hatching success is available in 23 of the studies; it ranged from 38.5 per cent with the Prothonotary Warblers in Michigan to 98.6 per cent with the Tree Swallows in Montana. In six of the studies hatching success fell in the sixties, in four in the seventies, in nine in the eighties and three in the nineties, the median value being 79 per cent.

Fledging success in the 32 studies ranged from 25.7 per cent with Prothonotary Warblers to 93.7 per cent with Weydemeyer's Tree Swallows. The average is 66.2 per cent. In one of the studies the percentage is in the twenties, in four it is in the forties, in two in the fifties, in ten in the sixties, in eleven in the seventies, in three in the eighties and in one in the nineties.

The very low figure for the Prothonotary Warblers in Michigan was due to competition with an over-population of House Wrens (Walkinshaw, 1941: 13). As to 44.5 per cent fledging success for Bluebirds, "predators are chiefly responsible for the loss of eggs, young, and brooding females. Cats and snakes regularly climb to the boxes; there has been some depredation by boys," (Laskey, 1943: 39); while *Solenopsis* ants have also caused losses (Laskey, letter). The high figure of success for Kendeigh's House Wrens reflects a protected environment with cats and snakes controlled. McAttee's area was also protected.

The only swallow in the table is *Iridoprocne bicolor* and it is represented by five studies, all but Weydemeyer reported in much detail. In Montana the birds never seem to have suffered from the weather in the nesting season. Nesting success in Connecticut reached 59.7, 69.2 and 75.6 per cent (Kuerzi). On Cape Cod it came to 56.5 (Austin and Low, 1932). 60.0 (Low, 1933a) and 36.3 per cent (Low, 1934). In central Massachusetts success ranged all the way from 16 to 61 per cent (Chapman). In all the years with poor suc-

TABLE 9.—Success of fourteen hole-nesting species

Species	Author	Years	Nests	Eggs	Hatched No. %	Fledged No. %
Tree Swallow, <i>Iridoprocne</i> <i>bicolor</i>	Chapman, '39 ¹	9	219	1123	928 83.4	679 61.0
	Low, '34	3	352	1759	1424 81.0	857 48.7
	Kuerzi, '41 ²	3	80	430	310 72.1	303 70.5
	Shelley, '37	2	37	184	163 88.6	123 66.8
	Weydemeyer, '35	8	60	363	358 98.6	340 93.7
Pied Flycatcher, <i>Muscicapa</i> <i>hypoleuca</i>	v. Haartman, '51	8	221	1074		789 73.5
Black-capped Chickadee <i>Parus</i> <i>atricapillus</i>	Odum, '41	2	11	74		53 71.6
Great Tit, <i>Parus major</i>	Gibb, '50 ³	5	202	1936	1653 85.4	1416 75.1
	Kluijver, '51 ⁴	19	5011	45466		29529 64.9
	Mackensie, '50	2	66	460	425 92.4	340 72.4
	Wolda, '29	2	623	6012	4579 76.2	3938 65.6
Blue Tit, <i>Parus</i> <i>caeruleus</i>	Gibb, '50 ³	5	183	1887	1548 82.0	1453 77.0
	Huxley, '38	2		247	185 75.0	168 68.0
	Kenrick, '40	4	37	286	187 65.0	128 44.7
	Mackensie, '50	2	46	413	366 88.6	327 79.2
Coal Tit, <i>Parus ater</i>	Mackensie, '50	1	18	161	153 95.0	131 81.4
House Wren, <i>Troglodytes</i> <i>aedon</i>	Kendeigh, '42 ⁵	19	1056	6773		5351 79.0
	Kuerzi, '41	3	34	211	135 64.0	118 55.2
	McAtee, '40	6		469		399 83.7
	Walkinshaw, '41	21	64	333	199 59.7	161 48.3
Bewick Wren, <i>Thryomanes</i> <i>bewicki</i>	Laskey, '46	15	21	129		79 56.8
Bluebird, <i>Sialia sialis</i>	Laskey, '43 ⁶	11	1401	6260	3943 63.0	2786 44.5
		2	86	377	302 80.1	274 72.7
	Musselman, '35 ⁷	3	301	1290		839 65.0
	Thomas, '46	9	67	272	213 78.3	172 63.2
	Walkinshaw, '41	20	50	203	131 64.5	127 62.5
Starling, <i>Sturnus</i> <i>vulgaris</i>	Lack, '48a			10557		7923 75.1
	McAtee, '40	6		472		410 84.5
Prothonotary Warbler, <i>Protonotaria</i> <i>citrea</i>	Walkinshaw, '41	11	121	413	159 38.5	106 25.7
	Walkinshaw, '41	2	36	163	100 61.3	100 61.3
House Sparrow, <i>Passer</i> <i>domesticus</i>	McAtee, '40	6		114		97 78.5
Five species	Wolda, '29 ⁸	2		755		500 66.2
Total				90,676		60,016 66.2

- ¹ Records for 1938-1943 given in letter by L. B. Chapman.
- ² Number of "nests" in Kuerzi's table XVI should read "Pairs"; 11 repeat nests are cited in table V and a second brood mentioned; total 80 nests.
- ³ Totals for 1947-1951 given in letter by J. A. Gibb.
- ⁴ Totals for 4 localities given in letter by H. N. Kluijver, observed for 12, 13, 14 and 19 years; number of complete sets 831, 1398, 941, 1841; number of eggs laid in complete sets 7676, 12909, 9037, 15844; number of young fledged 5080, 7793, 6649, 10007, percentage of success 66.2, 60.4, 73.5, 63.2, respectively.
- ⁵ See Nice, 1942.
- ⁶ Totals for 1938-1949 given in letter by Amelia Laskey.
- ⁷ With the addition of 67 eggs in 33 sets destroyed by April freeze, p. 120.
- ⁸ Great Tit, Blue Tit, Coal Tit, Redstart, *Phoenicurus phoenicurus*, and Wryneck, *Jynx torquilla*.

cess, both here and on the Cape, cold rainy weather during the nesting season brought starvation. The average success of the five studies involving 3859 eggs was 59.6 per cent. .

FACTORS INIMICAL TO NESTING SUCCESS OF THE MARTIN

Quarrels with other species over nesting sites, unfavorable weather, and attacks by parasites and predators constitute the chief difficulties encountered by the Purple Martin in reproducing its kind.

COMPETITORS FOR NESTING SITES

Five species of birds, three native, two introduced, have figured as competitors of Martins for nest houses.

Bluebird.—Wilson's friend, "the learned and venerable John Joseph Henry, Esq., judge of the supreme court of Pennsylvania," reported that for eight years Bluebirds took over the house erected for Martins and prevented the latter from using it (Wilson, 1812). Audubon (1831: 118) told of quarrels between the two species and of how he disposed of a Martin that persisted in disturbing the Bluebirds. Nuttall (1832: 599) wrote of the Martin, "Sometimes he ventures hostilities with the Blue-Birds and domestic Pigeons, whom he forces to abandon their hereditary claims."

In the seventies, Jacobs' (1909: 5) father erected a house of 16 rooms for Martins, but this was pre-empted by "another bird, one of beauty and courage," that "wanted the whole box for his single nest. Selfish, stubborn and stingy, he would drive away half a dozen of his own kind after they had assisted in breaking the Martin's eggs, or in killing the young. At first my father had my older brothers shoot some of these birds, but it seemed that another was always ready to take the place of one killed. Despairing of reducing the number of Bluebirds, my father ordered the shooting stopped. My brothers then caught the Bluebirds and pulled out their tail feathers, and thereafter whenever we saw a 'bobtailed' Bluebird in our part of town we

knew it was one that had visited our Martin house. Three years were spent in an effort to establish the Martins, but each spring the Bluebirds annoyed them so much that the Martins left. Finally my father took the box down." The region became built up and the Bluebird "became scarce, and in 1895 a March blizzard almost annihilated it."

Bluebirds still fight with Tree Swallows for nesting sites, but there seem to be few recent records in the East of competition with Martins. In South Deerfield, Mass., in May 1924, a flock of five or six Martins lingered about a farm "a day or two but were eventually driven off by Bluebirds," (Bagg and Eliot, 1937: 394). In Arkansas Thomas (1951) writes, "For years I have heard complaints that bluebirds take up the houses put up for purple martins. Shocking though it is, some people have shot bluebirds. . . . I can only suggest that plenty of houses suitable for both species be put up."

Tree Swallows.—Wilson (1812) wrote that this bird "often takes possession of an apartment in the boxes appropriated to the Purple Martin." In 1868 William Brewster (1906: 299) put up a box; Martins "visited it repeatedly and even attempted to enter the holes, but were invariably prevented from doing so by the Tree Swallows, which were numerous in the neighborhood and which quickly congregated and drove them away." In New England at the present time Tree Swallows have become well established in bird boxes and are a serious competitor with the larger, but less hardy Martin. Tree Swallows winter and nest further north than do Martins and subsist to some extent on berries, hence the adults are less vulnerable to severe weather than are the Martins.

"Tree Swallows have established large colonies," write Bagg and Eliot (1937: 392), "occupy all available houses before Martins come, and resent the occasional attempts of their larger cousins to lodge beside them. The mobbing of house-hunting Martins by Tree Swallows is an all too frequent sequel to the hopeful erection of a Martin-house." Three specific instances are noted of such occurrences in Massachusetts in 1919, 1932 and 1933.

An interesting observation was made by Kuerzi (1941: 14) in regard to his Tree Swallow colony. "Barn, Bank and Rough-winged Swallows (*Hirundo erythrogaster*, *Riparia riparia riparia*, and *Stelgidopteryx ruficollis serripennis*) breed very near the colony site, and during the spring migration Cliff Swallows pass through the area. All these species can freely enter the colony limits to feed or gather nest material without any molestation by the Tree Swallows. However, on June 11, 1938, a female Purple Martin entered the colony and was immediately set upon by the Tree Swallows. The whole colony was agitated for about 30 minutes, but the martin was soon mercilessly driven off."

House Wren.—This small bird does not try to drive Martins from their houses by direct attack, but it has often been reported as destroying its eggs. Widmann (1905) writes, "I would also say to those who put up bird houses of any kind to keep a watchful eye on the House Wren. He is as great a nuisance as the English Sparrow. He enters homes in the absence of the

owners, ruins their nests, pierces and throws out eggs and can do enough mischief in one season to threaten the existence of a whole colony of Martins."

Bagg and Eliot (1937: 418) speak of their puncturing Martin eggs, and Wallace (1927) mentions the same thing. "In Ann Arbor House Wrens destroyed two sets of eggs in a low Martin house." (A.)

House Sparrow.—The House Sparrow, *Passer domesticus*, introduced into America from Europe from 1850 to 1869, soon became abundant throughout the country. Aggressive, hardy and adaptable, it became a serious competitor to many of our native passerines, especially those nesting in cavities. Being a resident, it took over bird boxes before the return of the birds for which they were intended. An overwhelming amount of damaging evidence is presented by Barrows (1889); from Alabama to Illinois and Wisconsin came reports that English Sparrows "destroyed eggs of Martins," "threw out young," "killed young and old." Widmann is quoted as saying that in cool weather the Martins forage for food and Sparrows enter the nests and eat the eggs. Jacobs (1903: 19) tells of a male House Sparrow that killed seven Martin nestlings before he was able to shoot him with his 22 calibre rifle loaded with dust shot. "During the summer months I kill upwards of three hundred sparrows which I find paying attention to my martin houses." Since the nineties practically every book that mentions the Purple Martin laments the disastrous effect on its numbers of the introduction of the House Sparrow.

Martins were not always the victims. One of Barrows' correspondents in New York state said that the Martins dragged out sparrow nests with eggs and young and killed the latter. In discussing contests between the two species in Maine, Knight (1908: 45-) reported "Martins were proved victorious every time but once. . . . After the battle, the Martins busy themselves in throwing out the mass of hay, feathers and trash left by the Sparrows and incidentally any eggs or young which may be there."

Nicholson (1948) recounts how a Martin in Florida carried out a tiny Crested Flycatcher, *Myiarchus crinitus*, from a gourd, and re-entered the gourd despite the attacks of the parents. "Naturally the purpose was to evict the flycatchers to enable the invaders to possess this gourd for their own nesting activities."

The population of House Sparrows has decreased in the cities with the replacement of the horse by the automobile and also through competition with the Starling. In the meantime the bird has certainly become less aggressive.

"When I made a census of the Purple Martin in Ann Arbor in 1938 I found that every house containing Martins also had English Sparrows, and many houses that had no Martins had many Sparrows. But I also noted that even the combined population of the two species did not come near filling the room available and only rarely were more than half the rooms occupied in any one house.

"The Sparrows tend to keep out of the way of the Martins as much as possible while living in the same house. Usually they have their nests built before the Martins arrive and this bulky nest so fills a room that no Martin

will become interested in it. Once a Sparrow becomes settled in a room he is very persistent, and although he may avoid his enemies as much as possible, if fighting is necessary, he will fight and usually win. As long as the Purple Martins stay out of the room he has chosen, *the Sparrow shows no antagonism toward them*, and the Martins soon become accustomed to their neighbors and after the season is well begun, fights are few. The Martins seem to resent the Sparrows taking any conspicuous position on top of the house and will drive them away from such a place, while tolerating them in others.

"I observed one male Purple Martin that was unusually belligerent toward a pair of Sparrows nesting directly below him; he would sit on the porch in front of his room and look down at them and occasionally would make an attack. In order to see what would happen I closed all the rooms in the house except those occupied by Martins and two others, one on each side of this particular Martin. The Sparrows immediately took over one of these rooms and the male Sparrow on several occasions worsted the Martin. The interspecific fighting ability of Purple Martins is largely bluff and when the opponent fails to give in easily, they withdraw.

"Sparrows are dangerous competitors only in places where they are extremely abundant, as around farm buildings where there is a good food supply for them. In such places they will often take over a house and fill all the rooms before the Martins arrive. Unless the Martins have very active help, they will be driven out." (A.)

Starling.—The European Starling, *Sturnus vulgaris*, introduced into New York City in 1890, within 40 years had spread from the Atlantic to the Mississippi, nesting as far north as southern Canada and as far south as South Carolina. It has now reached the Pacific and is continuing to invade new breeding territories in the southern states. It is an even more serious competitor to the Martin than the House Sparrow.

"In 1938 I found that three out of 22 colonies of Martins had one or two pairs of Starlings. Many houses that had formerly contained Martins now had large populations of Starlings. From watching fights between the two species I believe that in almost every instance a Starling will drive out a Martin. The Martins remain in possession of many of their houses only because their human allies bring the forces of powder and shot against the enemy. It is difficult to drive out the Starlings even by shooting as they become exceedingly wild and gun shy. Fortunately, Starlings are not universally abundant and many owners of colonies have told me that they have had little trouble with them. Here, as with English Sparrows, it is the colonies around farm buildings that suffer most; the buildings usually afford nesting places and the fields and feeding lots plenty of food. Colonies of Purple Martins in residential districts are the least troubled." (A.)

WEATHER

Extremes of weather during the breeding season affect the Martins adversely: cold, rainy spells clear the air of insects, and young and sometimes adults will perish from starvation, while hot weather may drive the young prematurely from their nests.

Cold weather.—In western Pennsylvania Jacob's (1903: 20) colony suffered disaster in 1902 "when more than half the young died of starvation, superinduced by a cold wet spell which set in June 27th, just when many young birds were about old enough to leave their nests. This period lasted a week, during which time at least one hundred and fifty young and several old birds perished." Plate XI (1909: 41) shows three adults and 80 newly-hatched young that succumbed to a three-day cold wet spell in mid-June, 1903. "Where the parents themselves survived this unfortunate period they rebuilt their nests and brought out late broods."

Much more serious disasters took place in New England. Several such occurrences are mentioned as happening during the Nineteenth Century (Nuttall, 1832; Forbush, 1929), but the worst took place in June 1903 when the Martins in Massachusetts and contiguous parts of New England were nearly exterminated (Forbush, 1904; Brewster, 1906). Beseet by English Sparrows, Starlings and Tree Swallows they have never been able to regain a foothold. In 1929 Forbush wrote of the Martin's distribution in New England: "formerly common local summer resident in all the states, now uncommon, rare or wanting, or very local in most of southern New England and local in northern New England; most common in eastern Maine and locally in its southern counties," p. 139. In 1937 it was known to breed in only one locality—Gardner—in the Connecticut Valley in Massachusetts (Bagg and Eliot).

A very interesting study on the relation of weather to the life of the Swift, *Micropus apus*, was made by Koskimies (1950); he discusses the effects of cyclones, rain, wind and temperature on the numbers of insects and spiders in the air. He quotes from the experiments of the American Glick (1939) who studied the "aeroplankton" by sampling the air at different heights and under different weather conditions by means of airplanes. Insects were most abundant at 60 meters when the surface temperatures was between 21° and 27° C. (70° and 80° F.) A rise or fall of 10° C. (16° F.) "causes a decrease of insects to half the amount observed in optimal conditions," (Koskimies, 1950: 35). "During a rain period the food supply is practically completely interrupted." (1950: 45) Other studies on the distribution of insects in the atmosphere were conducted in Canada by Wellington (1945).

Hot weather.—In Missouri "Few Martins die during the first two weeks of their life, but the mortality is enormous during the following two or three weeks, when in a hot, dry season fully one-half were seen to perish. Exposed to a merciless July sun, tormented by innumerable parasites, half dead with the sting of an empty stomach, desperation seizes the poor bird, when it is seen to lose its hold and half falls, half flutters to the ground below. Once down it is lost. If not killed outright by the fall, it is soon found by an animal or, crawling under some sheltering object, starves to death. The parents were never seen to feed one on the ground. They content themselves with a short endeavor to make it fly up, but seeing that this is impossible they give it up for lost." (Widmann, 1922: 7)

This mortality during hot weather is a common experience. Jacobs speaks of 25 young perishing "from excessive heat" in 1901 (1903: 10)

"Many observers have noted that often young birds leave the nest before they can fly and since the parents do not feed them on the ground, they die. This has happened every year that I have had a colony under observation. I have on several occasions replaced these birds in the nest only to find them or some of their nest mates on the ground again a few hours later. Most of these young birds have fallen during periods of unusually hot weather—above 90° F. In no case have I found all the young from one nest gone in this manner; rather some will fall from every room. In one house in 1938 all the rooms lost young until each had only two left.

"It seems very probable that the heat coupled with a crowded condition in the nest room results in temperatures so high that the young are driven from the room and fall to the ground. *Most Martin houses have rooms too small for the needs of the birds.* People seem to want as many Purple Martins as possible and make rooms small so that there can be more of them in the house. The Martins themselves do not seem to have much judgment as to room sizes, for although they often take the larger rooms in a house first, they will return to small rooms in an old house year after year even though better houses are put up close by. It may be that larger rooms will minimize this loss of nestlings. In one house with rooms 6" x 7" x 8" only one young bird fell out." (A.)

INFERTILE AND ADDLED EGGS

Widmann remarks that the "remarkably large number of addled eggs, reaching as high as 20 to 25 per cent" in his colony might have been due to irregularities of incubation with the first-laid eggs (1922: 6).

"In 1938 and 1939 I found only three eggs that failed to hatch out of 79 laid. In 1940, 11 of 57 failed to hatch. Ten of these were in three clutches laid about 10 days earlier than any of the others; they were in a small colony by themselves." (A.)

PARASITES

In Missouri, "Soon after the first of July the heated dry period sets in and with its progress insect food adapted for nestlings becomes scarcer and scarcer, while the terrible scourge of the poor bird, its parasites, increases at an enormous rate. . . . The best prevention of such disasters [falling from the nest] is the free and often repeated application of insect powder, scattered over young and nest." (Widmann, 1922: 5, 7)

Widmann does not specify what parasites afflicted his birds. Peters (1933, 1936) lists two mites and two lice as taken from Purple Martins: *Dermanyssus gallinae* (Degeer), and *D. prognepphilus* Ewing, in Alabama; *Myrsidea dissimilis* (Kell.), and *Philopterus domesticus* (Kell.), both found on Martins in Michigan and New Hampshire.

"In the late summer of 1938 I was weighing daily 4 young Martins; I noted a few *Protocalliphora* [*Apaulina*] larvae on them at various times, but never more than two or three on a single bird. On the sixth day one of the birds ceased to gain and on the next day it was dead. Then two more birds

died on the eighth day and the last on the ninth day. Upon examining the nest I found 145 large larvae; they were identified as *Protocalliphora splendida* [*Apaulina metallica*]. During 1939 I found fewer of the larvae. In the late season of 1940 most of the nests were parasitized with these fly larvae and the loss of 13 young birds was attributed to them. In one nest where four small birds had died I found 294 larvae weighing 21.5 grams or about 20 per cent of the combined weight of the nestlings. It was quite cool when the birds were suffering from the parasites and their parents were having trouble finding enough food for them. The shortage of food undoubtedly contributed to their deaths. All attacks of these parasites have been on late broods." (A.)

PREDATORS

Bluebirds and House Sparrows have destroyed eggs and young of the Martin in the past; House Wrens punctured their eggs in Widmann's time and are still doing so.

Screech Owls, *Otus asio*, are believed to have been partly responsible for the disappearance of the Jacobs' Martin colony (Todd, 1940: 375). S. S. Dickey considers this bird 'the worst foe' of the Martin in West Virginia. It reaches into a house and extracts the nestlings. "I have known him to continue such ravages for an hour at least, taking as many as a half dozen martins to appease his ravenous appetite," (Bent, 1942: 505).

"In most Martin houses it is almost impossible for a mammal to climb from the pole supporting the house on to the house itself. I have seen Red Squirrels, *Sciurus hudsonicus loquax*, try several times but never with any success. An owner of a Martin colony in Ann Arbor told me that a Fox Squirrel leaped from a nearby tree onto the Martin house and took a young bird from the nest and killed it, whereupon he shot the squirrel. When Purple Martins nested in trees, squirrels were probably quite a factor in their lives." (A.)

Mrs. Commons wrote, "The flying squirrel is an especial enemy of the Martin when the boxes are not sufficiently in the open, and raccoons have been known to climb the pole and remove the young with their handy front feet." (Roberts, 1932, II: 55)

In Minnesota where Martins sometimes nest beneath boulders on islands, "sand-flies have been known to exterminate whole broods of young birds." (Roberts, 1932, II: 55).

Survival Problems of Adult Martins

Adult Purple Martins are exposed to many dangers, particularly in spring and at their fall roosts.

WEATHER

The Purple Martin hastens north, often far too early for its own good, and long before it starts to nest. Dependent as it is for food wholly on flying insects, this early arrival often spells disaster.

"Many writers have noted the danger that Purple Martins incur by coming so early in spring. The first arrivals, however, do not remain in a place when

conditions become unfavorable, but depart, presumably, to seek out a more desirable locality. Once the birds have settled in the colonies, cold weather will not drive them away. They seem able to withstand several days of cold weather and to be able to feed at surprisingly low temperatures, but cold weather takes a few birds every year." (A.)

In South Carolina, April 14 and 15, 1907, "large numbers died from cold and starvation during the prevalence of gales and cold weather." (Wayne, 1910: 138) That same year in western Pennsylvania: "The first one arrived at my premises April 3, and this one was killed by the unprecedented April freeze, which continued unceasingly until about the 19th of the month. During this period, all the Martins—at least a hundred, which had arrived in this locality, perished from cold and starvation." (Jacobs, 1909: 21)

Ten years later in Oberlin, Ohio, Martins arrived April 2; after a week of fair weather "there came nearly a week of rain and cold which caused the death of nearly all of them. Many were picked up dead or dying beneath the houses, others died within. All were hardly more than skeletons. Another lot arrived on the 14th and shared the same fate. Barn and Tree Swallows came within this flight, and while more of them survived, some were starved to death." (Jones, 1917b) Elsewhere Jones (1917a) writes of the continuing cold weather throughout most of May and "the great destruction of Purple Martins and Swallows during the first two weeks of May."

Again ten years later, in northern Minnesota, Martins arrived on April 11 to find cold, icy winds and everything frozen every night without "a sign of an insect of any kind." They starved to death and were picked up around the house and garage (Roberts 1932, II: 56).

In the Dakotas and Iowa "1950 may well go down as the year without a spring. . . . Purple Martins [lured north by a brief warm spell] appeared at their nesting boxes at the usual time in most places. Due to the unseasonable weather no insects were available and large numbers were found dead in and about their houses." (Gammel, 1950)

On Aug. 15, 1938 many Martins were killed in Chicago when the willow in which they were roosting was struck by lightning (Wright, 1939).

PREDATORS

Predators appear to play a minor role in the life of the adult Martin. The Food Habits file of the Fish and Wildlife Service contains one record of a Martin eaten by a Pigeon Hawk, *Falco columbarius*, one by a Marsh Hawk, *Circus cyaneus hudsonius*, and two by Sharp-shinned Hawks, *Accipiter striatus velox* (letter, W. H. Stickel). "Brewster (1937) records Martins falling prey to a Pigeon Hawk, while Oscar M. Bryens reports the same occurrence in a letter to Dr. Josselyn Van Tyne. Errington (1933) found the remains of a Martin beneath the nest of a Peregrine Falcon, *Falco peregrinus anatum*." (A.)

Linsdale (1928: 582) describes the reaction of Martins and other swallows to small hawks that attempted to catch them when feeding over a lake: "Whenever a hawk came all the swallows would gather into a compact flock which would rise and fly after the hawk until it retired."

Jacobs (1903: 20) describes how cats crouch in the grass "waiting for the birds to get to fighting and fall to the ground." "I (1909: 8) have been obliged to kill cats on three occasions for killing my Martins, and a neighbor informed me that a cat had captured two of his four nesting males at one strike."

DESTRUCTION BY MAN

Man destroys Purple Martins both by his inventions and deliberately.

Jacobs describes how several Martins died through striking telephone wires some 50 feet from one of the boxes; the substitution of heavily insulated wires, twisted together, made them easily visible and the trouble ended.

Two accounts of Martins killed on a low bridge spanning Albemarle Sound, North Carolina, have been published. On Sept. 10, 1940 "hundreds of dead" Martins were found there; the author suggested that they had been roosting on the railings "and flew into blinding headlights of cars as they traversed the sound." (Jacobson, 1947) Hill (1948), however, doubts this explanation. On Aug. 16, 1941, he "crossed this same bridge over Albemarle Sound just at sunset. A very large flock of Purple Martins were circling down and roosting on the timbers and rafters *under* the bridge, not on the railing. As we approached the southern end of the bridge, a threatening thunderstorm broke and the still circling birds were forced lower and lower until many were struck by the cars and a few landed unharmed but drenched on the highway. On returning on foot, we counted 173 birds on the bridge," all but two dead. "After dark, there were no birds on the railings or flying about, but many hundreds could be seen by flashlight on the timbers underneath the bridge."

Martins, like other birds, have long been subject to indiscriminate shooting, as lamented by Jacobs. In Oklahoma one of the males in our Martin house was shot by a boy who said he mistook it for a "blackbird." Murphy (1937: 31) writes that in South Carolina and Georgia it was "formerly shot for target practice and killed in large numbers, but this pernicious custom has, of recent years, been entirely discontinued." In West Virginia Johnston (1923: 60) reports that after the invasion of the English Sparrow Martins "began to disappear. Then the habit of shooting the night-hawk, commonly called 'bull-bat,' started, with the result that many reckless gunners also shot the martins, little realizing that both birds are man's great benefactors, for they destroy millions of mosquitoes and houseflies, which are among our most deadly enemies."

It is in their roosting habits that Martins sometimes conflict with human interests. They have been shot by police in Charleston, West Virginia (Johnston, 1923), while 8,000 to 15,000 were killed near Wilmington, North Carolina (Bent, 1942: 500). Johnston (1923) states that if an old tar barrel is burned where the fumes will reach the birds, they will quickly move their roosting place. It is reported that in Lincoln Park, Chicago, Martins are attacked in their roost on the excuse that they are "blackbirds."

Banding Purple Martins

Of 183 young Martins banded at the age of three weeks in the course of this study (at the George Reserve, Geddes Dam and Patterson Lake) two were recovered, one at the age of six weeks, the other two years later.

No. 38-244137, banded at Ann Arbor by R. W. Allen July 5, 1938, was found dead July 26, 1938, in Dexter Township, Mich., some eight miles northwest.

No. 38-244167, banded at Ann Arbor July 7, 1938, was found, probably dead, Aug 17, 1940, at Clio, Mich., 60 miles north of Ann Arbor. Since the date is too late for breeding, we cannot know where this bird nested and will have to classify the record under "migration."

In 1940, 80 records of returns and recoveries of Purple Martins were obtained from the Fish and Wildlife Service at Washington, D. C., through Mr. F. C. Lincoln; in 1949 others were obtained from Mr. Chandler Robbins and Mrs. Helen Webster of the Fish and Wildlife Service and directly through Rev. J. W. Baechle. The men who have done the most banding of this species are Oscar M. Bryens, McMillan, Luce Co., in the Upper Peninsula of Michigan; F. W. Rapp, Vicksburg, Kalamazoo Co., southwestern Michigan; J. W. Baechle, Collegeville, Indiana; and George Lowery, Jr., Baton Rouge, Louisiana.

Because of the wide ranging habits of the Martin in comparison to typically territorial species, it is difficult to evaluate records of birds found away from the natal or nesting colony. Jacobs wrote (1909: 24) "These birds travel over wide expanse in quest of food . . . and during their summer stay in this region, they, no doubt, roam over the whole county." Near Tucson, Arizona, most of the Martins that used the *summer* roost apparently came from nesting grounds in "the Sahuaro National Monument, an area of giant cacti twenty miles to the southeast" (Cater, 1944). None nested nearer than ten miles (A. Anderson, personal communication).

BANDING ADULT MARTINS

Returns and recoveries of 82 Martins, banded as adults, are shown in table 10. Each bird is counted only once, the last time time it was taken, no matter how many years it might have returned.

TABLE 10.—Data on purple martins banded as adults (individual returns)

	1	Years after Banding				Total
		2	3	4	5	
Breeding Season						
Home colony	44	17	11	3	2	77
10 miles distant	1					1
100 miles distant		1				1
Migration		1	2			3
	45	19	13	3	2	82

The great majority of these returns were trapped at the nesting box and released. Only five are definitely noted as dead.

"Widmann (1922: 2) suspected that Purple Martins returned to their former homes when, before he put up the boxes one spring he saw 'an old Martin hovering in the air at exactly the same spot and at the very same height above the ground where a box used to stand.' I have seen the same thing. The birds must have a highly developed sense of locality for I saw them flutter about a spot in the air, now vacant, that had held a Martin house the year before." (A.)

Of the 79 birds taken in the breeding season, 77 were found at the colony where they had been banded. As to the other two, both were banded at Fredericktown, Ohio, by Hicks (1933). The female, 3-46412, nested in June 1926, but the following year was found dead June 5, not far from a Martin house in Mt. Vernon, Ohio, 10 miles southeast of the place of banding. The male, 72541, was banded May 5, 1925, and raised young that year and the next in the same box. "On May 5, 1927, during a severe storm the bird was found with a broken wing at Hillsboro, Ohio," 100 miles southwest (as measured on the map). Hicks considers that both these birds had changed nesting sites, but there is no proof of this. The female might easily have been cruising around, while the male might have been blown a long distance in the storm.

The recoveries on migration are: a male banded at Vicksburg, Michigan, May 24, 1931, taken at South Bend, Indiana, March 14, 1934; a female banded at McMillan, Michigan, May 10, 1933, taken at Clayton, Alabama, April 16, 1936; and an adult "B219327, banded at Winona, Minnesota, May 30, 1934, by Elmer Ollhoff, 'found' in December 1936 near Itaituba on the Rio Tapacuragrande, Para, Brazil," (Cooke, 1938: 188).

Another recovery of particular interest is that of 40-273417, banded June 23, 1943, in Murfreesboro, Tennessee, by Henry O. Todd and shot by a Miskito Indian Oct. 6, 1943, in Cabo de Gracias a Dios, Nicaragua.

TABLE 11.—Purple martins banded as nestlings (individual returns)

	Age of Birds in Years								Total	
	1	2	3	4	5	6	7	8	No.	%
Breeding Season										
Home colony	8	8	4	3	3	2			28	61.0
8-22 miles away	3	2	1			1			7	15.3
28-58 miles away	4	1	3						8	17.7
100-200 miles away	1					2			3	6.3
Total	16	11	8	3	3	5			46	100.0
Migration	2	1	1	1		1		1	7	
Grand total	18	12	9	4	3	6	0	1	53	

BANDING YOUNG MARTINS

Data on 53 Martins banded as nestlings are shown in table 11 and figure 9. Twenty were reported as dead, six of these being taken on migration; this was doubtless true of some of the others.

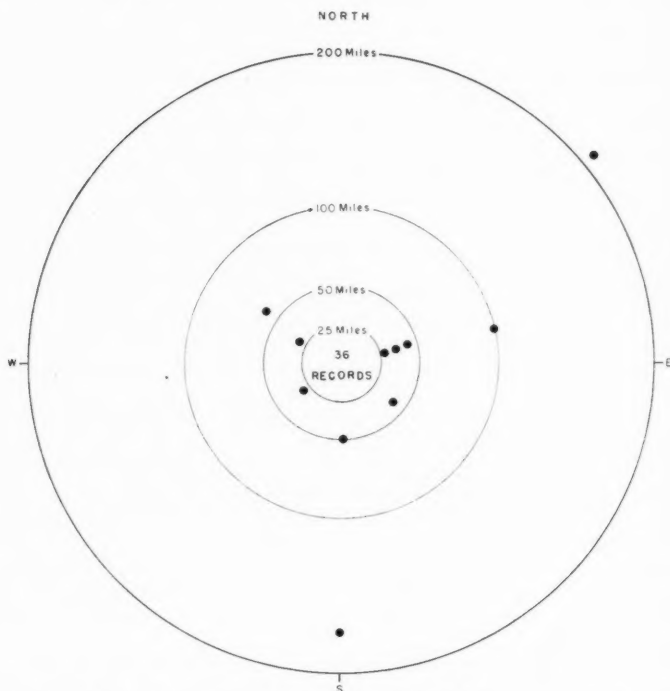


Fig. 9.—Relation of recovery of Purple Martins in the breeding season to birthplaces

The oldest individuals were two birds of six years and one of eight.

Of the 46 birds taken in the breeding season, 28 or 61 per cent, were found at the place of banding, seven others within 8 to 22 miles, eight within 28 to 58 miles, and three at distant points—100, 170 and 210 miles. With the far ranging habits of the Martin, it is possible that the birds found within 8 to 22 miles might have been nesting at or very near their birth place. The addition of these to the 28 would give 78.4 per cent return to the birth place.

It is difficult to evaluate the recoveries of the birds taken from 28 to 58 miles from the place of banding. There is no evidence of breeding with any of them. Arranged according to date of recovery, they are:

Banded at Vicksburg, Michigan, July 1, 1929, taken 50 miles south in Indiana, May 6, 1932.

Banded at Petal, Mississippi, June 11, 1940, found dead, 30 miles northwest, May 20, 1941.

Banded at Ohio, Illinois, July 4, 1940, found dead, 40 miles southeast, June 2, 1942.

Banded at Ardmore, Oklahoma, June 26, 1931, killed by car, 58 miles northwest, June 6, 1932.

Banded at Memphis, Tennessee, June 23, 1937, captured, died, 40 miles northeast, June 25, 1940.

Banded at Ohio, Illinois, July 10, 1931, taken 28 miles northeast, July 1, 1934.

Banded at Murfreesboro, Tennessee, June 29, 1939, found dead, 35 miles southwest, July 4, 1940.

Banded at Lockport, Louisiana, June 9, 1923, taken 35 miles northeast, July 15, 1924.

As to the long distance recoveries, two of them were reported by Cooke (1937, 1942); Mrs. Webster has given further information on these, correcting the place of banding of one, telling the age at banding of the other, and the distance and direction from the place of banding for both.

No. A286846 was banded at Columbia, Boone County, Missouri, June 18, 1932 by C. E. Northcutt, and was found dead at Hillview, Greene Co., Illinois, May 13, 1938, 100 miles east-northeast.

No. 240552, banded as a nestling at Winnipeg, Manitoba, July 31, 1924 by Andrew M. Davidson, was trapped in a Martin house and released unharmed at Fertile, Polk County, Minnesota, June 27, 1930, 170 miles south of Winnipeg.

As to the greatest wanderer, the bander, Oscar Gunnarson, informs me it was a nestling raised in his yard; 484214, banded July 23, 1928, at Lindsborg, Kansas, was picked up dead May 22, 1929 under a Martin house by George Hall, Glenwood, Iowa. Glenwood is 210 miles northeast of the place of banding.

Two of these were found by Martin houses, so they might have been nesting.

It seems as if the great majority of Martins return to the vicinity of the birthplace, but a very small proportion scatter widely.

RETURN OF YOUNG TO THE BIRTHPLACE

"Banding has thrown light on the much discussed question of the return of the young to the place they were hatched. Lincoln (1934: 152) says: 'What becomes of the young? While the mortality of juveniles is admittedly very high, nevertheless the only tenable answer is that they spread indiscriminately throughout the natural range of the species and it is pure chance if one should return to the area where hatched.'

"Most of the returns of young banded Purple Martins have been obtained by two banders, one in Vicksburg, Michigan and the other in McMillan, Michigan. If the young 'spread indiscriminately throughout the natural range of the species' I would expect to find as many of the young birds at Vicksburg appearing at McMillan as would return to Vicksburg and vice versa. Yet all

TABLE 12.—Returns and recoveries during the breeding season of birds banded as nestlings
(distance from banding locality in miles)

Species	Total	0-1		1-25		25-50		50-100		100-200		More than 200	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
American Robin, ¹													
<i>Turdus migratorius</i>	422	312	74.0	75	17.6	13	3.1	10	2.4	10	2.4	2	0.5
Purple Martin													
<i>Progne subis</i>	46	28	61.0	7	15.3	6	13.0	2	4.3	2	4.3	1	2.1
Barn Swallow, ²													
<i>Hirundo rustica</i>	97	56	57.7	34	35.1			4	4.1	3	3.1		
Tree Swallow, ³													
<i>Iridoprocne bicolor</i>	48	32	66.7	15	31.2	1	2.1						
Bank Swallow, ⁴													
<i>Riparia riparia</i>	35	17	48.5	18	51.5								
Pied Flycatcher, ⁵													
<i>Muscicapa hypoleuca</i>	88	63	71.6	25	28.4								
European Robin, ⁶													
<i>Erithacus rubecula</i>	90	50	55.6	39	43.5	1	1.1						

¹ Farner (1945). ² Boyd and Thomsen (1937). ³ Low (1934).

⁴ Stoner (1941). ⁵ Drost and Schilling (1940). ⁶ Lack (1948b).

ten recoveries of McMillan birds have been at McMillan and all the eight Vicksburg birds have appeared at Vicksburg." (A.)

If Lincoln's theory were true, Ruiter (1941: 207) calculates that with the Common Redstart, *Phoenicurus phoenicurus*, the return of a young bird to its birthplace could be expected once in 100,000 years. Instead, there appears to be an annual return of 23 percent of the surviving young of this species.

Table 12 shows returns and recoveries during following breeding seasons of 826 individuals of seven species banded as nestlings. The studies on the Tree and Bank Swallows were projects of individual banders and hence long distance recoveries would hardly be expected. The other five studies were compiled from the files of the central banding offices in North America, Great Britain and Germany. Results are summarized in the table, but further details on distance from the birthplace are of interest.

Of the European Barn Swallows, 26 were found within 2 to 6 miles of their birthplace, seven within 7 to 10 miles, and one at 13 miles. The long distance recoveries were as follows: four birds taken from 75 to 160 miles north, two taken at 82 and 125 miles south, and one 155 miles east. Of the Tree Swallows, twelve were captured nesting from 1 to 7 miles from their birthplace, and one each at 9, 11 and 32 miles. Eight of the Bank Swallows were caught in the home colony, seven were less than one-quarter mile distant, two were nesting between one-quarter and one mile away, twelve from 1 to 4 miles, and six from 5 to 9 miles. Twenty of the Pied Flycatchers were captured at boxes from 1 to 6 miles from their birthplace, four from 6 to 15, and one from 15 to 24 miles, as reported by v. Haartman (1949: 51). The data on the European Robins concern birds found dead. Forty were discovered at the place of banding, ten within one mile of it, 29 within 4 miles, six within 8 miles and the others at 11, 17, 17, 22 and 32 miles.

To sum up: in all these studies from one-half to three-quarters of the birds banded as nestlings and found in subsequent breeding seasons have been taken in the close vicinity of the birthplace. With the Tree Swallow and European Robin one bird of each species settled as far as 32 miles from its birthplace. With Barn Swallows, Purple Martins and American Robins a small number have settled at long distances from home, up to 160, 210 and 415 miles. With all seven species the majority of the young have returned to the exact or general location of the birthplace. With two species, single birds have been found at some distance (32 miles), and with three species a few have been taken at long distances from the birthplace (160 to 415 miles).

The Martin As a Social Bird

In his *Bird Societies* Friedmann (1935: 142) says, "We must distinguish between mere gregariousness and the presence of a harmonious system or society. No true social life has been observed among swallows." p. 163. On the whole, Swallows are more social than some colonial species for which the shortage of nesting sites seems to be the chief reason for closely-packed nesting and social defense is absent, as in some Alcidae. But Swallows are less social-

ly developed than birds that defend a common territory, build nests in common, or care for young collectively, as described by Friedmann.

Purple Martins have a strong social bond to one another. "In the spring before the beginning of the nesting season Martins usually hunt in groups, leaving the colony together and returning together." (A.) They are social in their migrating, roosting, and nesting.

MIGRATION AND ROOSTING

The social bond in Martins is strongest in late summer and fall when the birds gather in great companies to roost and to migrate, as described on pages 613-614 and 649.

In the spring several Martins usually arrive together. The first individuals are often called "scouts," and some people believe they go south again and return leading a band. Bagg (1937: 394) writes, "The existence of this scouting habit seems not to have been realized by our older ornithologists. Allen and Stearns gave May 1 to Sept. 1 as the Martin's season. But though it is indeed late April before any numbers of Martins arrive, a single male almost always comes many days earlier to make sure that the house is up and conditions propitious, and if not, to locate a better place for his group." This idea postulates a degree of intelligence and social responsibility that is not compatible with what we know of these birds. Martins do sometimes go south again in adverse weather, but we have no evidence that the "scouts" report on affairs to their waiting friends. In many other species some older males arrive exceedingly early on their nesting grounds. Why should not Martins do so?

NESTING BEHAVIOR

The relations of Purple Martins in the nesting season to fellow members of the colony besides their mates and young, and to birds of other species, will be briefly discussed under the subjects of territory, sexual fighting, and social defense.

The Function of Territory in the Purple Martin.—The Martin cannot be said to hold a group territory as is true with the Jackdaw, *Corvus monedula* (Lorenz, 1931, 1938) and Smooth-billed Ani, *Crotophaga ani* (Davis, 1940), where strangers of the same species are recognized and the whole colony unites to drive them away. The Martin's defense is individual, and is directed against intruders—other male Martins or birds of other species—that trespass on his porch or attempt to enter his room. The minimum space claimed by a Martin is one room and its porch, although many are able to hold more space, even in a crowded house. This type of territory—"Nesting station restricted to narrow surroundings of nest"—corresponds to Type D in Nice's classification (1943: 165).

"What is the function of this territory in the Purple Martin? Obviously it can have no food value, nor can it be said to prevent over-crowding. Rather, it seems to be a mechanism for bringing the sexes together and insuring each pair a place to nest." (A.)

Swallows are typically colonial birds, although a few nest singly and are even markedly territorial. This seems to be true of the Blue-and-White Swallow (Skutch, letter), Rock Martin (Niethammer, 1937), Red-throated Rock Martin (Moreau, letter), and Pacific Swallow (Meyer, 1934). The Barn Swallow was found by Davis (1937) to hold a territory of 2.5 feet around a nest.

Sexual Fighting.—Fighting in defense of a room is described on pages 617-618; fighting in defense of a mate, on page 621. Tinbergen (1936) defines "sexual fighting" as "all fighting occurring shortly before and during the formation of sexual bonds."

"Sexual fighting occurs in Purple Martins under two conditions: first, when an individual's room in the colony is invaded; and second, when one male approaches the mate of another away from the house. In the first case, the fighting is very determined and often prolonged and it is always between individuals of the same sex, males fighting with males, females with females. But I have never seen both members of one pair fight with both members of another pair at the same time. This fighting seems in every way homologous with the sexual fighting among the more typically territorial birds like the Snow Bunting or Reed Bunting. The same purpose is served, that of retaining an area necessary for the pair if it is to successfully carry out reproduction. This type of fighting is restricted to the place that one individual owns and another covets; once away from this particular spot, the two birds that fought so fiercely a few minutes before perch side by side with no sign of animosity.

"The second type of fighting differs considerably from the first. It coincides with the period during which copulation is taking place and does not seem to be linked with any particular place. Rather it seems to be a case of sexual jealousy when the male does not wish any other male near his mate. Possibly this is an adaptation to colonial life where a number of males are always near any female and promiscuity would be easy." (A.)

Social Defense.—"The vigor with which Martins drive off avian enemies from the neighborhood of their breeding colonies has been described by almost every writer that mentioned the bird. In the virtually hawkless and owl-less world of today an ornithologist seldom has the privilege of witnessing this behavior. But I have seen Blue Jays, *Cyanocitta cristata*, driven from the vicinity of the colony a number of times. One Jay in particular persisted in returning to a telephone wire that was a favorite perch of the Martins. Almost as soon as he had alighted, some Martin would perceive him and immediately give chase. He was easily driven back to the underbrush where the Martins did not care to follow, whereupon the pursuer would return to the house or fly to a perch on the wire. In less than a minute the Jay would return and be driven away again, sometimes by the same and sometimes by another Martin. Strangely enough, the birds of one colony would attack American Bitterns, *Botaurus lentiginosus*, but ignore Great Blue Herons, *Ardea herodias*. These attacks are pure bluff in that the Martin never strikes the enemy either with feet or beak; they simply swoop over the individual and scream and attempt to confuse him.

"The birds will attack cats and dogs beneath their house, and also a man that climbs to their home. Swooping down to a few inches above his head, they will emit a loud cry as they pass over. When a large colony is visited there is considerable commotion on the first appearance of the intruder, but after a short time most of the birds settle on convenient perches and express their disapproval by a great deal of chatter. A few individuals may return to the attack at short intervals, but they soon go back to their perches and after 15 or 20 minutes the visitor will be entirely unmolested. Larger groups have a better chance of protection because of the many individuals to attack a common enemy.

"It seems to me that Martins act as individuals rather than as a group. An attack could be made much more effective by a mass attack instead of by a few individuals attacking and then flying away, while others may or may not take up the battle.

"At the beginning of the season, attacks are of short duration and mild in nature; their intensity increases as the season progresses, reaching a height just before the young leave the nest. After the young have departed there is a rapid decline in intensity of attack, although defense is continued as long as the birds remain. Purple Martins will often join their neighbors in other colonies during times of danger. Several times while on a ladder examining a Martin house I have counted several more birds circling and screaming in the air above me than were living in the colony." (A.)

ASOCIAL BEHAVIOR

"When the young make their first flights, the adults are apt to chase and harry them. Widmann (1922: 8) wrote: 'The Martins themselves know well the importance of this step, and a young bird's first appearance on wing never fails to create general commotion in the colony. Some of them, taking delight in the chase, follow the fledgling, and in their endeavor to drive it to a safe place often harass the poor thing until its strength gives out and it falls.' To me the process seems a direct attempt to attack the young rather than drive it to a safe place.

"Shelley (1934) tells of a rogue female Tree Swallow that killed 25 young birds of this species in his colonies. I believe that similar happenings are not rare among Purple Martins. Several people have told me they have seen old Martins throw young from the house. I saw this only once. On this occasion I was told by the owner of a Martin colony that he had just seen an adult male throw three young birds from a house. We replaced the nestlings, which did not seem to be hurt much by their fall, to the room from which he said they had been taken. A little later an adult male appeared on the scene, entered the room and came out with a young bird in his bill. He flew out over a near-by lake and dropped the nestling 30 feet from shore. He immediately returned for the second and then the third, both of which he treated in the same way." (A.)

Summary

The Purple Martin, largest of North American Swallows, is sexually dimorphic, but the first year male looks much like the female. It is highly social in its nesting, roosting, and migration. In eastern North America man has largely destroyed the primeval trees in which it used to nest; he now offers homes to this bird, his original motive being to utilize its services in driving off birds of prey. Dependent as it is on a highly specialized nesting site for which competition is keen, it often returns from its wintering grounds in Brazil too early for its own good. It is highly vulnerable to weather in the matter of food supply.

Migration of the Martin is closely correlated with temperature. The mean temperature of the day of arrival at four stations was $5^{\circ}\text{--}14^{\circ}\text{ F.}$ above normal; of the week before arrival at three stations $6^{\circ}\text{--}7^{\circ}$. Average dates recorded for 5 to 55 years from south to north show the gradual progress of spring migration from February 6 in Florida to April 29 in North Dakota. In two localities very early colonies averaged seven and eight days earlier than more typical ones. Two instances of reverse migration are cited.

In the West, Martins still nest in cavities in large dead trees; the Southwestern Martin in saguaros. In man-made houses it is essential that rooms be made large to prevent loss of nestlings during hot weather.

The male defends a room from other males; the female chooses a room and thereby obtains a mate.

Nest building may not begin for more than a month after the arrival of the first birds at a colony. The date of its start is correlated with temperature. At first males are more active, later females. While the females gather material from the ground, their mates guard them from other males.

From 4-6 eggs are laid. There is but one brood in the South as well as the North.

Incubation is by the female alone; she spends some 70 per cent of the daylight hours on the nest in normal weather, about 80 per cent in colder weather. The male guards the nest during her absences. Incubation lasts 15-16 days. In table 4, 14 species of swallows are compared as to weight of adult, role of sexes in incubation, number of eggs laid, length of incubation and fledging. With North Temperate Zone species incubation lasts 14-16 days, with Tropical species 14-20 days. In table 5 it is shown that where only the female incubates, eggs are covered from 69-77 per cent of daylight hours in the North Temperate Zone, from 49-60 per cent in the Tropics; when both parents incubate, this percentage is over 90 per cent in the North, from 70-90 in the Tropics.

Fledging usually takes 28 days. In the first 12 days the nestling increases from less than 3 grams to about 45 grams; at 20 days it weighs about 57 grams; at 28 days 50 grams. From the 12th to 20th day the bird grows most of its feathers. Widmann watched 16 boxes for a whole day; 3277 trips were made, 55.6 per cent of them by the females. Hourly trips per young ranged

from 1.9 for week-old birds and 5 for four-week birds to 6.2 for five-week birds, averaging 4.4 trips for all ages.

Nesting success during three years at the George Reserve was poor, only 38.5 per cent of the eggs developing into fledged young. In 32 studies of 14 other hole-nesting species reproductive efficiency ranged from 25.7 per cent with Prothonotary Warblers in Michigan to 93.7 per cent with Tree Swallows in Montana. The average success of 90,676 eggs came to 66.2 per cent.

Among factors inimical to nesting success are unfavorable weather—cold and rain that bring starvation, heat that drives the young prematurely from the nest, and attacks by parasites, chiefly calliphorid larvae. Predators play a minor role, but conflicts with nest-competitors may be crucial. In the past Bluebirds were a menace; House Sparrows when first introduced were very aggressive; Tree Swallows and Starlings drive Martins from houses, while House Wrens pierce their eggs.

Adult Martins may perish from cold weather in early spring and in the nesting season. Predators do not capture many of these swift flying birds. But Martins are killed by various of man's inventions and deliberately in their roosts.

Of 79 Martins banded as adults and recovered in the breeding season, 77 were found at their home colonies, one was taken 10 miles away and another 100 miles, the latter during a severe storm. One Martin banded in Minnesota was taken $2\frac{1}{2}$ years later in Brazil. Of 46 Martins banded as nestlings and recovered from May to July from one to six years later, 28 were taken at their birthplace, seven from 8-22 miles distant, eight from 28-58 miles distant, one 100 miles northeast, one 170 miles south, one 210 miles northeast. In banding studies on seven species from one-half to three-quarters of the birds banded as nestlings and found in subsequent breeding seasons have been taken in close proximity to the birthplace. The greatest age attained by a banded Martin is eight years.

Pages 655-658 deal with some aspects of the Purple Martins' social behavior: whether old males act as "scouts" in the spring, the function of territory in this species, the questions of sexual fighting and social defense, and finally a case of intraspecific destruction of young.

REFERENCES

- ANDERSON, A. H. AND A. ANDERSON 1946—Notes on the Purple Martin roost at Tucson, Arizona. *Condor* 48: 140-141.
- ANDERSON, R. M. 1907—The birds of Iowa. *Proc. Davenport Acad. Sci.* 11: 125-417.
- AUDUBON, J. J. 1831-1839—*Ornithological Biography*, 5 vols., Edinburgh.
- AUSTIN, O. L., JR. AND S. LOW 1932—Notes on the breeding of the Tree Swallow. *Bird-Banding* 3: 39-44.
- BAERG, W. J. 1931—Birds of Arkansas. *Agri. Exp. Sta. Bull.* 258: 1-196.
- BAGG, A. C. AND S. A. ELIOT, JR. 1937—Birds of the Connecticut Valley in Massachusetts. Northampton, Mass. pp. 1-813.
- BAILEY, F. M. 1928—Birds of New Mexico. *N. M. Dept. Game & Fish pp.* 1-807.

- BARROWS, W. B. 1889—The English Sparrow (*Passer domesticus*) in North America. Bull. U. S. Bur. Biol. Surv. No. 1, 405 pp.
- 1912—Michigan bird life. Mich. Agri. Coll. pp. 1-822.
- BARTEL, K. E. 1945—Purple Martins in Blue Island. Aud. Bull., Ill. Aud. Soc. No. 56: 4.
- 1947—Increase of Purple Martins. Ibid. No. 61: 5-6.
- BENT, A. C. 1942—Life histories of North American Flycatchers, Larks, Swallows and their allies. U. S. Nat. Mus. Bull. 179: 1-555.
- BOYD, A. W. AND A. L. THOMSON 1937—Recoveries of marked Swallows within the British Isles. British Birds 30: 278-287.
- BREWSTER, W. 1906—The birds of the Cambridge region of Massachusetts. Mem. Nuttall Orn. Club, 4. Cambridge, pp. 1-426.
- 1937—October farm. Harvard Univ. Press, Cambridge, pp. xv+285.
- CASH, J. A. 1933—Tree Swallows: some observations made at close quarters. Bird-Lore 35: 201-205.
- CATER, M. B. 1944—Roosting habits of Martins at Tucson, Arizona. Condor 46: 15-16.
- CATESBY, M. 1731-43—The natural history of Carolina, Florida and the Bahama Islands. 2 vols., C. Marsh, London: 100, 100 pp.
- CHAPMAN, L. B. 1935—Studies of a Tree Swallow colony. Bird-Banding 6: 45-57.
- 1939—Studies of a Tree Swallow colony. Ibid. 10: 61-72.
- CLARK, T. C. AND M. M. NICE 1950—William Dreuth's study of bird migration in Lincoln Park, Chicago. Chic. Acad. Sci. Special Pub. 8: 1-43.
- COOKE, M. T. 1937—Some returns of banded birds. Bird-Banding 8: 144-155.
- 1938—Some interesting recoveries of banded birds. Ibid. 9: 184-190.
- 1942—Returns from banded birds. Igid. 13: 110-119.
- COUES, E. 1878—Birds of the Colorado Valley. U. S. Geol. Surv. of the Territories Misc. Publ. 11: xvi+807.
- CRAIGMILE, E. A. 1939—A popular bird roost. Illinois Audubon Bulletin No. 30: 13-15.
- DAVIS, D. E. 1940—Social nesting habits of the Smooth-billed Ani. Auk 57: 179-213.
- DAVIS, E. M. 1937—Observations on nesting Barn Swallows. Bird-Banding 8: 66-72.
- DE BRAEY, L. 1946—Auprès du nid de l'Hirondelle de Cheminée *Hirundo rustica* Linné. Le Gerfaut 36: 133-198.
- DROST, R. AND L. SCHILLING 1940—Über den Zug des Trauerfliegenschneppers, *Muscicapa hypoleuca* (Pall.). Ber. Ver. Schles. Ornith. 11: 71-85.
- DUTCHER, W. 1920—The Purple Martin. Nat. Assoc. Aud. Soc. Ed. Leaflet No. 13: 49-52. In Portraits and habits of our birds, 1920, ed. by T. G. Pearson. Nat. Assoc. Aud. Soc., N. Y.
- EDSON, J. M. 1943—A Study of the Violet-green Swallow. Auk 69: 396-403.
- FABLES, D. 1950—Fourteenth Breeding-Bird Census. Pine Barrens and Cedar Bog. Audubon Field Notes 4: 301.
- ERRINGTON, PAUL L. 1933—Food habits of southern Wisconsin raptors. Part II. Hawks. Condor 35: 19-29.
- FARNER, D. S. 1945—The returns of Robins to their birthplaces. Bird-Banding 16: 81-99.
- FISHER, G. C. 1907—A Purple Martin roost. Wilson Bull. 19: 119.
- FORBUSH, E. H. 1904—The destruction of birds by the elements in 1903-04. Fifty-first Ann. Rep. Mass. State Bd. Agri. pp. 457-503.
- 1929—Birds of Massachusetts and other New England States, 3. Mass. Dept. Agri., Boston. pp. 1-466.
- FRIEDMANN, H. 1935—Bird societies, from A handbook of social psychology. Worcester, Mass., pp. 142-184.

- GABRIELSON, I. N. AND S. G. JEWETT 1940—Birds of Oregon. Oregon State Coll. pp. 1-650.
- GAMMELL, DR. AND MRS. R. T. 1950—Spring Migration. Northern Great Plains Region. Audubon Field Notes 4: 248.
- GIBB, J. 1950—The breeding biology of the Great and Blue Titmice. Ibis 92: 507-539.
- GLICK, P. A. 1939—The distribution of insects, spiders and mites in the air. Tech. Bull. 673. U. S. Dept. Agric. pp. 1-150.
- GRINNELL, J. AND T. I. STORER 1924—Animal Life in the Yosemite. Univ. California Press. pp. 1-752.
- HAARTMAN, L. VON 1949—Der Trauerfliegenschnäpper. 1. Ortstreue und Rassenbildung. Acta Zool. Fenn. 56: 1-104.
- 1951-2—Populationsprobleme. Ibid. 67: 1-60.
- HALL, D. G. 1947—The Blowflies of North America. Thomas Say Foundation pp. 1-477.
- HAMILTON, C. E. 1909—How to attract Martins. Bird-Lore 11: 231.
- HICKS, L. E. 1933—Returns of Purple Martins. Bird-Banding 4: 113.
- HILL, N. P. 1948—Purple Martins killed on a bridge. Auk 65: 448-449.
- HOWARD, H. E. 1929—An introduction to the study of bird behavior. Cambridge, Univ. Press, pp. xii+136.
- HOWELL, A. H. 1924—Birds of Alabama. Dept. Game and Fisheries, Montgomery, pp. 1-384.
- 1932—Florida bird life. Fla. Dept. and Fresh Water Fish pp. 1-579.
- HUXLEY, J. S. 1938—Nests and broods in Whipsnade Sanctuary in two successive years. Proc. Zool. Soc. London A: 108: 445-452.
- JACOBS, J. W. 1903—The story of a Martin colony. Gleanings No. 2: 1-24. Waynesburg, Pa.
- 1909—The Purple Martin and houses for its summer home. Ibid. No. 5: 1-44.
- JACOBSON, M. A. 1947—Purple Martins killed on a bridge. Auk 64: 457.
- JOHNSTON, I. H. 1923—Birds of West Virginia. State Dept. Agri., Charleston, W. Va. pp. 1-138.
- JONES, L. 1903—The birds of Ohio. Spec. Pap. Ohio State Acad. Sci. No. 6: 1-241.
- 1917a—The May migration, 1917 at Oberlin, Ohio. Wilson Bull. 29: 103-104.
- 1917b—The season. Oberlin region. Bird-Lore 19: 212.
- KENDEIGH, S. C. 1942—Analysis of losses in the nesting of birds. Jour. Wildlife Management 6: 19-26.
- Parental care and its evolution in birds. Cont. Baldwin Research Lab. 44. (In press).
- KENRICK, H. 1940—A study of Blue Tits by colour ringing. British Birds 33: 307-310.
- KIMBALL, H. H. 1921—Notes from southern Arizona. Condor 23: 57-58.
- KLUIJVER, H. N. 1951—The population ecology of the Great Tit, *Parus m. major*. Ardea 39: 1-135.
- KNIGHT, C. R. 1908—The Birds of Maine. Bangor, Maine, pp. xvii-673.
- KOSKIMIES, J. 1950—The life of the Swift, *Micropus apus* (L.), in relation to the weather. Ann. Acad. Scient. Fenn. Ser. A. IV. Biol. (15): 1-151.
- KUERZI, R. G. 1941—Life-history studies of the Tree Swallow. Proc. Linn. Soc. N. Y. 52-53: 1-52.
- LACK, D. 1940—Courtship feeding in birds. Auk 57: 179-218.
- 1948a—Natural selection and family size in the Starling. Evolution 2: 95-110.
- 1948b—Notes on the ecology of the Robin. Ibis 80: 252-279.
- LASKEY, A. R. 1943—The nesting of Bluebirds banded as nestlings. Bird-Banding 14: 39-43.

- 1946—Some Bewick Wren nesting data. *Migrant* 17: 39-43.
- LINCOLN, F. C. 1934—The operation of homing instinct. *Bird-Banding* 5: 149-155.
- LINSDALE, J. M. 1928—Birds of a limited area in eastern Kansas. *Univ. Kansas Science Bull.* 18(11): 517-626.
- LORENZ, K. 1931—Beiträge zur Ethologie sozialer Corviden. *Journ. f. Ornith.* 79: 67-127.
- 1938—A contribution to the comparative sociology of colonial-nesting birds. *Proc. 8th Int. Orn. Cong., Oxford*, pp. 207-218.
- LOW, S. 1933a—Further notes on the nesting of the Tree Swallows. *Bird-Banding* 4: 76-87.
- 1933b—Notes on the nesting of Bluebirds. *Ibid.* 4: 109-111.
- 1934—Nest distribution and survival ratio of Tree Swallows. *Ibid.* 5: 24-30.
- MACNAMARA, C. 1917—The Purple Martin. *Ottawa Naturalist* 31: 49-54.
- MACKENSIE, J. M. D. 1950—Nestling mortality amongst tits on Tentsmuir, 1949 and 1950. *British Birds* 43: 393-398.
- MAYR, E. AND J. BOND 1943—Notes on the generic classification of the Swallows, *Hirundinidae*. *Ibis* 85: 334-341.
- MCATEE, W. L. 1940—An experiment in songbird management. *Auk* 57: 333-348.
- MCCONNELL, T. L. 1918—High mortality among the Purple Martins in western Pennsylvania during April, 1917. *Bird-Lore* 20: 130-131.
- MEARNS, E. A. 1890—Observations on the avifauna of portions of Arizona. *Auk* 7: 251-264.
- MEYER, O. 1934—Bruten von *Hirundo tahitica frontalis* Qu. G. Beiträge z. Fortpflanzungsbiologie d. Vögel 10: 141-143.
- MOREAU, R. E. 1939a—Numerical data on African birds' behaviour at the nest: *Hirundo s. smithii* Leach, the Wire-tailed Swallow. *Proc. Zool. Soc. London Ser. A.* 109: 109-125.
- 1939b—Parental care by some African Swallows and Swifts. *Bull. Brit. Orn. Club* 59 (424): 145-149.
- 1940a—Numerical data on African birds' behaviour at the nest.—II. *Psalidoprocne holomelaena massaica* Neum., the Rough-wing Bank-Martin. *Ibis* 14th Ser. 4: 234-238.
- 1940b—Incubation and fledging periods of African birds. *Auk* 57: 313-325.
- 1947—Relations between number in brood, feeding-rate and nestling period in nine species of birds in Tanganyika Territory. *Jour. Animal Ecol.* 16: 205-209.
- AND W. M. MOREAU 1939a—Observations on Sand Martins at the nest. *British Birds* 33: 95-97.
- 1939b—Observations on Swallows and House-Martins at the nest. *Ibid.* 33: 146-151.
- MURPHY, E. E. 1937—Observations on the bird life of the Middle Savannah Valley, 1890-1937. *Contr. Charleston Mus.*, 9, Charleston, S. C. pp. vii+61.
- MUSSELMAN, T. E. 1935—Three years of Eastern Bluebird banding and study. *Bird-Banding* 6: 117-125.
- NICE, M. M. 1935—Same mates for six years. *Ibid.* 6: 42.
- 1937—Studies in the life history of the Song Sparrow I. *Trans. Linn. Soc. N. Y.* 4: 1-247.
- 1941—"Courtship feeding in birds." *Auk* 58: 56.
- 1942—Review of Kendeigh. *Bird-Banding* 13: 90.
- 1943—Studies in the life history of the Song Sparrow II. *Trans. Linn. Soc. N. Y.* 6: 1-328.
- 1947—Review of DeBraey. *Bird-Banding* 18: 174-175.
- AND R. T. THOMAS 1948—A nesting of the Carolina Wren. *Wilson Bull.* 60: 139-158.

- NICHOLSON, D. J. 1948—Nest-robbing behaviour of the Purple Martin. *Auk* 65: 600-601.
- NIETHAMMER, G. 1937—Handbuch des deutschen Vogelkunde I. Akad. Verlagsgesellschaft M.B.H. Leipzig. pp. xxiv+474.
- NUTTALL, T. 1832—Manual of the ornithology of the United States and Canada, I. Hilliard and Brown, Cambridge, pp. viii+683.
- OBERHOLSER, H. C. 1917—A remarkable Martin roost in the city of Washington. *Bird Lore* 19: 315-317.
- 1919—Another Purple Martin roost in the city of Washington. *Ibid.* 21: 96-99.
- 1938—The bird life of Louisiana. Dept. Conservation, State of Louisiana Bull. 28: 1-834.
- ODUM, E. P. 1941—Annual cycle of the Black-capped Chickadee—2. *Auk* 58: 518-545.
- PETERS, H. S. 1933—External parasites collected from banded birds. *Bird-Banding* 4: 68-75.
- 1936—A list of external parasites from birds of the eastern part of the United States. *Ibid.* 7: 9-27.
- PURCHON, R. D., D. WOODWARD AND P. K. WICKSTEAD 1948—The nesting activity of the Swallow. *Proc. Zool. Soc. London* 118: 146-178.
- RAPP, F. W. 1926a—Migration of the Purple Martin at Vicksburg, Michigan. *Auk* 43: 375-376.
- 1926b—Nesting data of Purple Martin at Vicksburg, Michigan. *Ibid.* 43: 550.
- ROBERTS, T. S. 1932—The birds of Minnesota, 2. *Mus. Nat. Hist. Univ. Minn.* pp. 1-821.
- RUITER, C. J. S. 1941—Waarnemingen omtrent de levenswijze van de Gekraagde Roodstart, *Phoenicurus ph. phoenicurus* (L.) *Ardea* 30: 175-214.
- SHELLY, L. O. 1934—Tree Swallow tragedies. *Bird-Banding* 5: 134.
- 1937—Further Tree Swallow notes. *Ibid.* 8: 80-81.
- SKUTCH, A. 1945—Incubation and nestling periods of Central American birds. *Auk* 62: 8-37.
- SMITH, W. P. 1937—Further notes on the nesting of the Barn Swallow. *Ibid.* 54: 65-69.
- STEVENS, O. A. 1950—A migration list from Fargo, North Dakota, 1910-49. *Flicker* 22: 90-104.
- STONE, W. 1937—Bird studies at Old Cape May, 2. Delaware Valley Ornith. Club, Philadelphia pp. 521-941.
- STONER, D. 1936—Studies on the Bank Swallow (*Riparia riparia riparia* Linnaeus) in the Oneida Lake region. *Roosevelt Wild Life Annals* 4: 126-233.
- 1941—Homing Instinct in the Bank Swallow. *Bird-Banding* 12: 104-109.
- TAVERNER, P. A. 1933—Purple Martins gathering leaves. *Auk* 50: 110-111.
- THOMAS, R. T. 1946—A study of Eastern Bluebirds in Arkansas. *Wilson Bulletin* 58: 143-183.
- 1951—With the Country Diarist. *Arkansas Gazette* Jan. 28.
- TINBEGEN, N. 1936—The function of sexual fighting in birds; and the problem of the origin of "Territory." *Bird-Banding* 7: 1-8.
- 1939—The behaviour of the Snow Bunting in spring. *Trans. Linn. Soc. N. Y.* 5: 1-95.
- TODD, W. E. C. 1940—Birds of western Pennsylvania. Univ. Pittsburgh Press, pp. xv+710.
- TRAUTMAN, M. B. 1940—The birds of Buckeye Lake, Ohio. *Misc. Publ. Mus. Zool. Univ. Mich.* No. 44: 1-466.
- VAN ROSSEM, A. 1914—Notes from the San Bernardino Mountains. *Condor* 16: 145-146.

- 1936—Notes on birds in relation to the faunal areas of South Central Arizona. Trans. San Diego Soc. Nat. Hist. 8(18): 123-146.
- WALKINSHAW, L. H. 1941—The Prothonotary Warbler, a comparison of nesting conditions in Tennessee and Michigan. Wilson Bulletin 53: 1-21.
- WALLACE, T. R. 1927—A House Wren despoils a Purple Martin nest. Ibid. 39: 232.
- WAYNE, A. T. 1910—Birds of South Carolina. Contr. Charleston Mus. 1, Charleston, S. C., pp. xxi+254.
- WELLINGTON, W. G. 1945—Conditions governing the distribution of insects in the free atmosphere. Canad. Entom. 77: 7-15, 21-28, 44-49, 69-74.
- WEYDEMEYER, W. 1934—Tree Swallows at home in Montana. Bird-Lore 36: 100-105.
- 1935—Efficiency of nesting of the Tree Swallow. Condor 37: 216-217.
- WHEATON, J. M. 1882—Report on the birds of Ohio. Rep. Geol. Surv. Ohio. 4: 187-628.
- WIDMANN, O. 1884—How young birds are fed. Forest and Stream 22: 484.
- 1905—Nest-box notes. Bird-Lore 7: 17-18.
- 1922—Extracts from the diary of Otto Widmann. Trans. Acad. Sci. St. Louis 24(3): 1-77.
- WILLIAMS, G. C. 1950—Weather and spring migration. Auk 67: 52-65.
- WILSON, A. 1812—American ornithology, 5. Bradford and Inskeep, Philadelphia, pp. xii+13-122.
- WITHERBY, H. F., F. C. R. JOURDAIN, N. F. TICEHURST AND B. W. TUCKER. 1938—The handbook of British birds, 2. Witherby, London, pp. xiii+352.
- WOLDA, G. 1929—Verslag van de Ornithologische Afdeeling over het Jaar 1928. Plantenziektenkundige Dienst, Wageningen pp. 1-27.
- WOOD, N. A. AND A. D. TINKER 1934—Fifty years of bird migration in the Ann Arbor region of Michigan, 1880-1930. Occ. Papers Mus. Zool. Univ. Mich. No. 280: 1-56.
- WOODBURY, A. M., C. COTTAM AND J. W. SUGDEN 1949—Annotated check-list of the birds of Utah. Bull. Univ. Utah 39(16): 1-40.
- WRIGHT, E. G. 1939—Gathering of the Martins. Aud. Bull. Ill. Aud. Soc. No. 31: 1-3.
- ZIEGLER, C. J., JR. 1923—Notes on a Purple Martin colony. Auk 40: 431-435.

A Contribution to the Life History and Ecology of the Plethodontid Salamander *Aneides aeneus* (Cope and Packard)*

Robert E. Gordon**

The Highlands Biological Station and Biology Department, University of Georgia, Athens

CONTENTS

Acknowledgements	667	Post hibernation aggre-	
Procedures and results	667	gation and dispersal	688
General distribution		Population dynamics	689
and habitat selection	667	Preliminary experiments with	
Intensive study of colonies	670	vital limits of water loss	691
Habitat and		Procedure	691
community relationships	673	Results	693
Life history and annual cycle	679	Discussion	694
Breeding period	679	Summary	693
Dispersal and aggregation	687	References	700
Hibernation	688		

With the appearance of Emmett Reid Dunn's monograph, *The Salamanders of the Family Plethodontidae*, in 1926, the taxonomy of this important family was greatly clarified. Dunn points out, as do subsequent authors, that the Appalachian highlands of the eastern United States is the place of origin of the family. This is the region where the most primitive forms are now found, and where the most primitive species occupy what is presumed to be the original habitat niche, the mountain brooks (Hairston, 1949). During the course of evolution within the Plethodontidae, varying degrees of adaptation to terrestrial life have developed and now some species remain on land throughout their life cycle: these species do not return to water to breed as do many amphibians which have developed the terrestrial habit for the adult stages. Among the plethodontid genera in the eastern United States the genus *Aneides* is the most terrestrial. Four species and two subspecies belonging to this genus are recognized at the present time. Only one of these—*A. aeneus*—occurs in the eastern United States; the others, *A. ferreus*, *A. f. flavipunctatus*, *A. f. niger*, *A. l. lugubris* and *A. l. farallonensis*, are western forms, principally from California and Oregon. A fifth species, *A. hardii*, has been

* A thesis submitted to the graduate faculty of the University of Georgia in partial fulfillment of the requirements for the degree of Master of Science.

** Present address, Department of Zoology, Tulane University, New Orleans, La.

recently proposed (Lowe, 1950). Dunn (1926) considers *A. aeneus* as the most primitive member of the genus.

While making a distributional study (summer of 1948) of salamanders of the southern Appalachians in western North Carolina, north Georgia and western South Carolina, Gordon and Smith (1949) located several colonies of *Aneides aeneus* in the vicinity of Highlands, North Carolina. Preliminary observations were made on one of these colonies. A more systematic study was begun during the summer of 1949. It was planned that this study should cover a complete annual cycle of the species, thereby gaining information on the life history of this primitive and little known species which might shed light on the evolution and ecology of the genus and on the development of terrestrial adaptations in the Plethodontidae.

ACKNOWLEDGEMENTS

I am indebted to a large number of individuals for assistance during this investigation. For pertinent suggestions relative to the nature of the investigation and for the privilege of using their distributional data the writer is extremely grateful to Dr. Sherman C. Bishop, University of Rochester; Professors Maurice Brooks, West Virginia University; N. Baynard Green, Marshall College; Mr. Glenn Gentry, Tennessee Department of Conservation; Dr. Arnold B. Grobman, University of Florida, and Dr. Clifford H. Pope, Chicago Natural History Museum, as well as many others. Drs. Irwin C. Kitchin, University of Georgia and Kenneth Wagner, Florida State College, have aided very much with the photography. For suggestions and aid in connection with the laboratory experiments which are a part of this study, sincere thanks go to Dr. Charles C. Wilson, University of Georgia. Dr. Don L. Jacobs, University of Georgia, has been very helpful in the identification of liverworts and mosses. I owe much to my wife, Catherine T. Gordon, who has contributed in field work and in typing of the manuscript.

Special thanks are accorded the Highlands Biological Station, its director, Professor Thelma Howell, and friends, for without the financial aid provided through the Ward Fellowship (1948) and the Margaret Cannon Howell Scholarship (1949 and 1950) the work would have been impossible.

Finally, I am indebted to Dr. Eugene P. Odum, Biology Department, University of Georgia, for his advice, criticism and encouragement, throughout the course of study.

PROCEDURES AND RESULTS

The study is divided into three parts, (1) summary and analysis of the general distribution and habitat selection of *A. aeneus*, (2) intensive study of the life history and population dynamics of two colonies of this salamander at Highlands, North Carolina through one complete annual cycle, and (3) preliminary experimental work to determine resistance to drying of *Aneides* and its probable closest competitor.

GENERAL DISTRIBUTION AND HABITAT SELECTION

In addition to the author's personal observations in the field and the examination of published records, many persons known to have collected *Aneides* were written to in order to obtain as complete a picture of the overall distribution of the species as possible. All of these data were used in constructing a habitat-distribution map. *Aneides aeneus* seems to be confined to the Appalachian Plateau and the Blue Ridge Provinces (as delineated by Fen-

neman, 1938). No records exist for the Appalachian Valley, creating thereby an apparent hiatus between the areas of known distribution (see fig. 1).

The following locality records for the nine states in which *A. aeneus* is known to range are supported either by citation of author (s), or by museum*

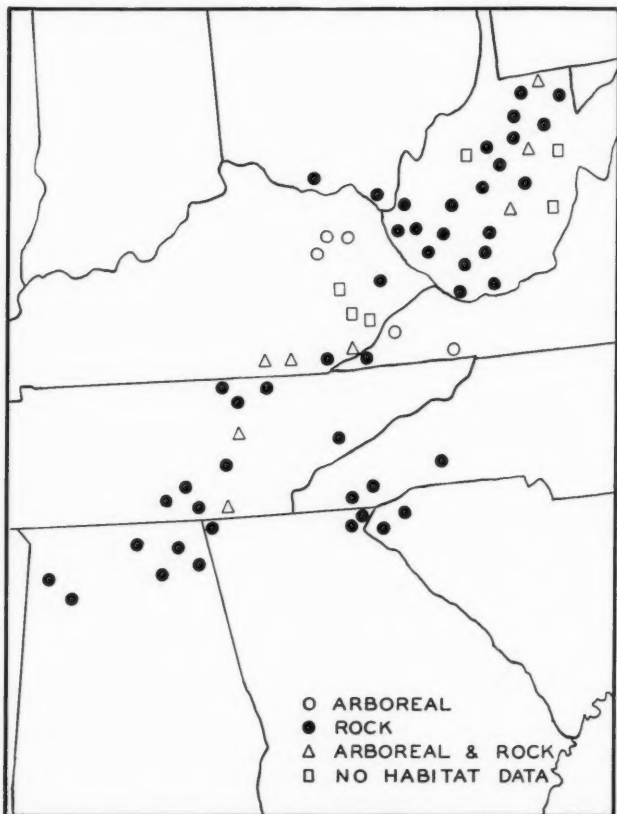


Fig. 1.—Habitat-distribution map of *Aneides aeneus* (Cope and Packard)

* Abbreviations for the various museums and individual collections cited are as follows: American Museum of Natural History (A.M.N.H.); Academy of Natural Sciences, Philadelphia (A.N.S.P.); Carnegie Museum (C.M.); Chicago Natural History Museum (C.N.H.M.); Cincinnati Society of Natural History (C.S.N.H.); Collection of Robert E. Gordon (R.E.G.); University of Georgia Museum of Zoology (U.G.M.Z.); University of Michigan Museum of Zoology (U.M.M.Z.); United States National Museum (U.S.N.M.).

specimens. The author has not examined specimens in collections other than his own and that of the University of Georgia. In all cases where habitat information was obtainable this is also indicated.

Alabama: *DeKalb County*—Mentone, "under buildings and rocks in dark damp places along the riverfront" (Penn, 1940); *Franklin County*—15 miles east of the state line (U.M.M.Z. 88588) *Jackson County*—Sand Mt. at Long Island, "in rocky bluff woods" (Holt, 1924); *Madison County*—Huntsville (Loding collection, Bishop, personal correspondence, 1950); *Marshall County*—Sand Mt. (U.S.N.M. 75050); *Winston County*—near county line between Haleyville and Carbon Hill, in sandstone crevices (C.M. 19924-26).

Georgia: *Dade-Walker counties*—Lookout Mountain (C.M. 17851); *Rabun County*—Bascom's Cave, Raven Rock Mt., rock crevices (R.E.G. 318-319); *Rabun-Habersham counties*—Tallulah Gorge, rock crevices (Bishop, 1928; Gordon and Smith, 1949).

Kentucky: *Bell County*—North side of Pine Mt., 5.6 miles east of Pineville, rock crevices (U.M.M.Z. 95743); *Breathitt County*—near Calla (C.S.N.H. 1681); *Elliot County*—Little Sandy River near Ordinary, "beneath bark of black gum tree" (Welter and Barbour, 1940); *Floyd County*—Estill, rock crevices (N. B. Green, personal correspondence, 1950); Estill (U.M.M.Z. 86583); Estill (C. M. 18119-21); *Harlan County*—Pine Mt., northern base, "loose bark of dead trees" (Pope, 1928); Pine Mt. (C.N.H.M. 57413-5; U.M.M.Z. 75506; C.M. 10934; A.M.N.H. 41624-29, 41637-42, 41790, 44963, 45117-20, 45218, 50162, 40130-37); near Cumberland (C.S.N.H. 1709); Big Black Mt. near Virginia line (C.S.N.H. 2512); Pine Mt., 1 mile north of Cumberland, sandstone crevice (Barbour, personal correspondence, 1950); *Letcher County*—near Whitesburg (C.S.N.H. 1696); *Menifee County*—near Pine Ridge, "rotten basswood stump in Rhododendron thicket" (Welter and Barbour, 1940); *McCreary County*—near Whitley City (C.S.N.H. 1648); inhabits both arboreal and rock habitats (Gentry, personal correspondence, 1949); *Perry County*—near Breathitt County line (C.S.N.H. 2500); one half mile west of Knott county line (C.S.N.H. 2520); *Rowan County*—near head of Christy Creek, "beneath bark of a fallen butternut tree" (Welter and Barbour, 1940); *Whitley County*—Cumberland Falls State Park, cliffs, undersides of ledges (Hubricht, personal correspondence, 1949).

North Carolina: *Jackson County*—Granite City, rock crevices (Gordon and Smith, 1949); *Macon County*—Highlands, south slope of Satulah Mt., rock crevices (R.E.G. 314, 321-22; U.G.M.Z. 33-40); *Rutherford County*—Bat Cave, rock habitat (Weller, 1930a).

Ohio: *Adams County*—one half mile east of Stouts, Green Township, rock crevices (Walker and Goodpaster, 1941; U.M.M.Z. 85557); *Smokey Creek*, Green Township, rock habitat (U.M.M.Z. 95930); *Lawrence County*—one half mile north of Burlington, Fayette Township, under rocks or rock crevices (U.M.M.Z. 95942, 95943).

South Carolina: *Oconee County*—Jocassee (R.E.G. 278); *Pickens County*—Sassafras Mt., rock crevices (Charleston Museum, E. B. Chamberlain, personal correspondence, 1950); Pinnacle Mt. (Brimley, 1927; Pickens, 1927).

Tennessee: *Bledsoe County*—rock habitat (Gentry, personal correspondence, 1949); *Cumberland County*—arboreal and rock (Gentry, *ibid.*); *Fentress County*—Allardt, Buffalo Cove, (1300 ft.) tributary of the Obie River, rock crevices (U.M.M.Z. 59048; Gentry, 1941); *Franklin County*—rock crevices (Gentry, personal correspondence, 1949); *Grundy County*—rock crevices (Gentry, *ibid.*); *Hamilton County*—Lookout Mt., large rocks (Green, personal correspondence, 1950); *Sawyer's Springs* on Walden Ridge, arboreal (Rhoads, 1895); *Marion County*—Nickajack Cave (Type Locality) rock (A.N.S.P. 10461, TYPE, Cope and Packard, 1881); *Smallmouth* mouth of Nickajack Cave, rock cliff (U.M.M.Z. 95742); *South Pittsburgh* (U.S.N.M. 18025); *Pickett County*—rock crevices (Gentry, 1941, and personal correspondence, 1950); *Scott County*—Big South Fork of Cumberland River at White Oak Creek (U.M.M.Z. 63078); *Sevier County*—Eastern slope of Mt. Leconte (Weller, 1930b; C.S.N.H. 363).

Virginia: *Lee County*—Dolomite caves of Cumberland Mts. (U.S.N.M. 16660:

Dunn, 1926); *Washington County*—Clinch Mt. near Hayter Gap, arboreal (Fowler, 1947); *Wise County*—High Knob, six miles south of Norton, arboreal (C.N.H.M. 56911-4; Pope, personal correspondence, 1949); High Knob Recreation Area, Powell Mt., east of Norton, arboreal (Hubricht, personal correspondence, 1950).

West Virginia: *Barbour, Boone, Braxton, Cabell, Clay, Fayette, Gilmer, Harrison, Kanawha, Lewis, Lincoln, Logan, McDowell, Marion, Mercer, Raleigh, Wayne, Webster and Wyoming counties*—rock crevices (Maurice Brooks, personal correspondence, 1949); *Monongalia, Nicholas and Upshur counties*—arboreal and rock habitat (Maurice Brooks, *ibid.*); *Boone County*—Peytona (C.M. 61635-6); *Calhoun County*—two miles above Grantsville (C.M. 15361-2); *Kanawha County*—Hudnall, Big Indian Cave (C.M. 19326-7); Holly Grove (C.M. 7461-4); Alum Creek (U.S.N.M. 84175); *Lincoln County*—Fourteen Mile Creek, 7 miles above Ranger (C.M. 19422-2); one mile north of Myra (C.M. 16069-70-89); *Logan County*—near Blair (C.M. 16134); 2 miles east of Mallory (C.M. 16111); *McDowell County*—2 miles southeast of Panther (C.M. 15962-64); 2 miles south of Panther (C.M. 15954); *Marion County*—near Hammond (C.M. 12759-66); Gladly Creek Gorge below Rock Lake (C.M. 14175-6); *Mercer County*—southeast of Bluefield on U. S. 21 (C.M. 14418); 2 miles east of Maeboury (C.M. 15821); *Monongalia County*—Cooper's Rock, rock habitat (C.M. 19382, 16989, 16965; C.N.H.M. 25011-2; Netting and Richmond, 1932); Cooper's Rock, arboreal and rock habitat (Brooks, personal correspondence, 1949); *Nicholas County*—Camp Woodbine (C.M. 15449-56); near Lockwood, Panther Mt. (C.M. 12675); 2 miles east of Summersville, rock habitat (Brooks, 1948); near Richmond (C.M. 12078-80); 4 miles south of Summerville (C.M. 7510); *Pocahontas County*—Cranberry Mt. (C.M. 7470); Droop Mt. State Park (C.M. 21184, 21199, 21200, 21202); *Preston County*—1 mile north of Rockville, Sandy Creek, in spring house, but area surrounded by "massive sandstone formations" (C.M. 24414-16); *Randolph County*—6 miles west of Elkins (C.M. 15726-7); 5 miles west of Elkins (C.M. 15687); 4 miles west of Elkins (C.M. 15676); 5 miles south of Elkins (C.M. 15671); 2 miles from Norton, Rich Mt. (C.M. 12849-50); Rich Mt. above Norton (C.N.H.M. 27816-7); *Upshur County*—French Creek (C.M. 11147); *Wayne County*—1 mile east of Louisa (C.M. 18146-7); 1 mile north of Echo (C.M. 16047-8); 4 miles northeast of Fort Gay (C.M. 16030); 3.5 miles northeast of Fort Gay (C.M. 16012-3); 3.5 miles northwest of Fort Gay (C.M. 16010-1); 3 miles south of Wayne (C.M. 6078); *Wyoming County*—Baileysville (U.S.N.M. 33621-2).

In most cases where two or more localities exist in a single county, only one is indicated on the map.

INTENSIVE STUDY OF COLONIES

Procedure.—During the spring and summer of 1949, a study area was set up (near the Highlands Biological Laboratory, Highlands, North Carolina) for the intensive study of a colony of *A. aeneus*. This area consisted of a plot of land of approximately 1.10 acres, or 47,800 square feet (hereafter referred to as the Highlands Study Area), and was divided into twenty-one units of approximately equal size. Each unit was designated by a number. Within the unit, the available rock crevices which might be used by the organism were numbered. The number was painted (white) on the rock adjacent to the crevice. Thus, in referring to any individual crevice, the designation might be unit 15, crevice number 2, or 15#2. A border, or buffer area containing similar rock crevices, surrounded the Highlands Study Area on two sides. Beyond this border, no colony of *Aneides* existed for a distance of approximately one and one third miles airline. A map of the Highlands Study Area was made, indicating unit and crevice numbers (Fig. 2).

Observations were begun on April 30, 1949. For the first few weeks the

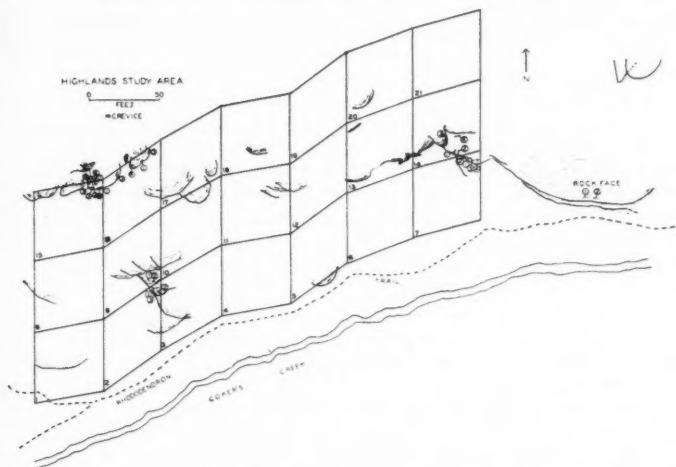


Fig. 2.—Sketch map of the Highlands Study Area indicating the position of crevices by encircled numbers. Unit numbers are located in the lower left hand corner of each unit.

entire area was examined until a knowledge of the units containing suitable habitat for the salamander was obtained. After this time, those units lacking suitable habitat were checked every other week during the summer months and on each monthly visit during the rest of the year. Following these preliminary observations weekly visits were made to the area during the months of June, July and August, 1949, (except during the first two weeks of June and last week of August, when daily observations were made), and monthly trips during the fall, winter and spring months of 1949-50. During June 1950, daily observations were made from the seventh through the twenty-first of the month.

Another area (hereafter referred to as the South Satulah Area) was located on the south slope of Satulah Mountain, fifty yards below North Carolina Highway 28. This consisted of a large cliff with several smaller rock outcrops in the general vicinity. The crevices here were also numbered with white paint. Studies made on this area supplemented the work on the Highlands Study Area. Observations were made at the same rate as those on the Highlands Study Area except that during the early part of June 1949 and 1950, visits were made every other day.

Observations on the two areas were carried out both during the day and night. Except during the month of June 1950, no regular hour for visiting the areas was maintained.

Other localities visited occasionally included, Tallulah Gorge and Bascom's Cave, Rabun County, Georgia; Granite City, Jackson County, North Carolina; and Jocassee, Oconee County, South Carolina.

A total of 438 individual observations of adults, immature and young were made on the Highlands Study Area during the course of the investigation. Thirty-seven individuals were marked and released. The released specimens were sexed, measured and the unit and crevice from which they were captured was recorded. Sexing in the field was accomplished by separating the cloacal lips and examining for fine papillae anteriorly with the aid of a small hand lens. Males possess this distinctive character, while the female vent is smooth (Bishop, 1943). During the breeding season, females could be distinguished by the obvious white ovarian eggs which can be readily seen by pressing the abdomen dorso-laterally, while at other periods in the cycle they can be recognized by the smoothness of the vent. Measurements in the field could be made with an accuracy of plus or minus one millimeter.

A marking system was utilized to facilitate recognition of each animal on recovery. Because of the unusually well developed phalanges found in the genus *Aneides*, a method of "toe clipping" was used.* A laboratory experiment involving toe clipping of two adult males and one immature specimen was carried out to determine whether regeneration would occur. Over a seven week period no regeneration of toes was noted. This method was utilized in the field for thirteen months with only one sign of regrowth, and that abnormal. The same marking and recapture methods were employed on the South Satulah Area, where fifteen of a total of forty-four individuals captured were marked. Clipping of as many as two toes apparently did not seriously affect the activity of the organism. Specimens collected in six localities exhibited no signs of a similar accidental mutilation.

Environmental data were obtained by use of a Taylor's field thermometer (1948), a Taylor's maximum-minimum thermometer and a Bendex Friez recording hygro-thermograph, Model 594, (1950). Regional weather data were obtained from the official Highlands U. S. Weather Bureau Station, located 3 miles south and five hundred feet lower than the Highlands Study Area. The thermometers were placed directly in the crevice, generally within six inches of a female *Aneides* and her eggs. The hygro-thermograph was maintained in the immediate vicinity of one of the larger granite outcrops in the Highlands Study Area. Reading of the maximum-minimum thermometer on the Highlands Study Area was made as near 10:00 A.M. as possible each morning. That of the South Satulah Area was made at 11:30 A.M. on every other day. The recording hygro-thermograph was checked by use of a sling psychrometer every other day while in use.

In order to ascertain the floristic components, a strip transect was made on the Highlands Study Area, beginning at the edge of Coker's Creek and working through units 3, 10 and 17 (see fig. 2). A reconnaissance of the South Satulah Area was made to estimate the dominant plants.

Results.—The results of the intensive study of the two colonies and observations at four other localities may be dealt with under the three categories:

* The toes were numbered counterclockwise beginning with the left hind foot. The smallest toe on each foot was disregarded in the numbering, thus giving a total of 14 toes. In referring to marked specimen 1-9, we would be speaking of the outermost toes on the left hind and right front feet.

habitat and community relationships, life history and annual cycle, and population dynamics.

Habitat and community relationships.—The Highlands Study Area is located in a rich cove on the south slope of Bear Pen Mountain and begins about forty-three feet from Coker's Creek. The slope of the area averaged forty-one per cent. The lower boundary of the area followed "Rhododendron Trail" which runs ENE-SSW, approximately parallel with the creek. In the more moist places and along the edge of the stream the trees, in order of dominance or abundance, were *Tsuga canadensis*, *Acer rubrum* and *Magnolia fraseri*. *Liriodendron tulipifera* was of sporadic occurrence in the ravine below. Other trees of occasional occurrence on the dryer portions of the slope were *Carya glabra*, *Quercus alba*, *Quercus borealis*, *Quercus montana*. The understorey was composed of dense stands of *Rhododendron maximum* in the vicinity of the stream and lower two-thirds of the area. *Kalmia latifolia* replaced this on the upper third. Scattered throughout were occasional specimens of *Hamamelis virginiana* and *Nyssa sylvatica*. Sprouts of *Castanea dentata* were found around the occasionally occurring stumps. In open sunny areas, the predominant shrubs were *Vaccinium* sp. and *Leucothoe* sp. *Hydrangia* sp. was of occasional occurrence. In order of dominance the herbaceous cover was provided by *Galax aphylla*, *Dennstaedtia punctilobula* and *Viola* sp. *Lysimachia quadrifolia*, *Chimaphila maculata*, *Clintonia umbellata*, seedling *Rhododendron*, *Kalmia* and *Smilacina* were other herbs of lesser occurrence. *Trillium catesbaei* and *Anemone quinquefolia* support the herbaceous layer during the spring and early summer months.

In some units on the Highlands Study Area where *Rhododendron* was so dense as to allow very little penetration of light, no herbaceous layer occurred. *Smilax rotundifolia* was the only liana encountered, and together with *Rhododendron* frequently made very dense thickets.

Where outcrops of granite occurred, seedlings of *Rhododendron* and various other plants were abundant. *Asplenium montanum* was a common fern in crevices, or on ledges, of the outcrops at six localities visited during the study. Exposed and generally dry outcrops were occupied by the pioneering species of *Grimmia* and *Cladonia*. The large foliose rock tripe or "nigger head," *Umbilicaria* sp., with some individual thalli of over two decimeters, is characteristic of very dry, exposed outcrops. On ledges where the moisture supply is intermittent, the large leafy liverwort, *Diplophyllum spiculatum* and a moss, *Plagiothecium* sp. form extensive mats. Another leafy liverwort, *Scapania nemorosa*, together with a moss *Dicranella* sp. spread upon wetter surfaces in mat form. *Dicranella* and *Dicranum fuscescens* are two common mosses found to invade crevices. The prothallia of *Asplenium* is another crevice invader.

The South Satulah Area, consisting of a large cliff lacking the protection afforded by the ravine at the Highlands Study Area, was subject to a greater amount of insolation. The trees in order of dominance were as follows: *Carya glabra*, *Acer rubrum*, *Quercus montana*, *Hamamelis virginiana*, *Quercus borealis*, *Quercus alba*, *Cornus florida* and *Liriodendron tulipifera*.



Fig. 3.—A winter illustration of the dense cover provided by hemlock and Rhododendron in a typical ravine in which outcrops are frequently located

Vaccinium sp., *Kalmia latifolia* and *Azalea calendulacea* dominated the understory. Herbs included *Fragaria virginica*, *Oenothera biennis*, *Polygonatum* sp., *Trillium Catesbaei*, *Viola* sp. and *Galax aphylla*. *Smilax rotundifolia* was abundant at the base of the cliff.

Figure 3 suggests the type of vegetative cover of the Highlands Study Area.

Gordon and Smith (1949) summarized the types of rock on which *A. aeneus* has been reported. They concluded that, "the type of rock apparently is not a limiting factor but its geological condition as to crevices, their depth and position appear to be important." During the course of study, repeated searches at six localities in the southern Blue Ridge Mountains revealed no *Aneides aeneus* living in dead trees, standing or fallen. The only specimen ever seen on a tree was an immature individual crawling down a small dead oak sapling which was leaning against a fractured granite outcrop along Clear Creek in Rabun County, Georgia. Brimley (1941) reports the occurrence of a single individual in the woodpile of Dr. W. C. Coker (located approximately 100 feet from the Highlands Study Area). Bishop (1928) reports the finding of a single specimen hiding beneath a piece of bark lying on the surface of a rock several feet above the ground in Tallulah Gorge. Hence *A. aeneus* apparently dwells almost entirely in crevices of rock outcrops in the southern Blue Ridge region, occasionally wandering overland for short distances (see below).

From observations made at the two study areas and four other localities, two general types (as to their use by the salamander) of crevices were found to occur. These may be designated as breeding, or egg laying crevices, and transitory crevices. Breeding crevices may also be transitory, but transitory crevices have never been observed to be used for breeding purposes. Table 1 summarizes the data obtained from the two study areas on all crevices in which *A. aeneus* was observed. Data presented for the Highlands Study Area are the result of observations for a three year period, while those from the South Satulah Area represent only two years of observations. Measurements were made at the mouth of the crevice, care being taken to measure the largest portion of the opening. Those crevices with a height of more than 1.5 inches generally have a V-shaped profile, so that they become narrower toward the rear.

In general the breeding crevices are moist but not wet, and admit little or no water from surface run off. This also holds true for the majority of transitory crevices. The invasion of moss into a crevice resulted in its abandonment as a breeding site in every case where this was observed to have occurred. However, such mossy crevices might be used in a transitory capacity (see Table 1).

No specimens were observed in crevices completely exposed to sunlight. Where occupied crevices were partially exposed for a portion of the day (South Satulah Area, Fig. 4), their depth was sufficient to allow the salamander to withdraw to the cooler interior. Shading, either by vegetation or overhanging cliffs is essential for all habitats observed by the author. The use of a flashlight was frequently required in order to see the salamanders in the crevices.

Temperature data from within and near a typical breeding crevice, together with data from the official weather station, are presented in Table 2. The recording hygro-thermograph was placed about eight feet from crevice 15#2 and a maximum-minimum thermometer was placed in the crevice about six inches away from the eggs.

High temperatures are frequently more critical to an organism than low ones. The "buffering effect" of the crevice is indicated by the difference of 5.6° F. in maximum temperature between the crevice and the outside general environment. Comparison of the temperatures taken near the crevice with those of the U. S. Weather Bureau Station show a difference of 4.0° F. in regard to the maximum, and -0.1° F. minimum. Gordon and Smith (1949) reported the average temperature for five days (June 16 to 21) in 1948 in seven breeding crevices on the Highlands Study Area to vary only slightly from 18° C. (64.4° F.). Temperature readings made every other day in a breeding crevice on the South Satulah Area averaged 71.1° F. for the maximum and 58.1° F. for the minimum, with 52 to 72 for the extremes. The relative humidity (as recorded by the above mentioned hygro-thermograph) ranged between 100 and 61, with average maximum and minimum being 99.1 and 75.3, respectively. The annual precipitation recorded by the Highlands Weather Station is 82.63 inches. The periods of greatest average precipitation

occur during summer and winter months. Some of the mountain districts of North Carolina and extreme northeast Georgia have more rainfall than any other region in the eastern United States (Yearbook of Agriculture, 1941). The Highlands region is near the center of one of these areas of high precipitation.

TABLE 1.—Data on individual crevices containing *Aneides* from the Highlands and South Satulah Study Areas for three summers, 1948, 1949, 1950

	Breeding Crevices		Transitory Crevices	
	Highlands	Satulah	Highlands	Satulah
Number	10	6	18	12
Average width*	8.7	17.3	7.8	12.3
Average height	1.1	.83	.72	.65
Extremes width	3-23	1-34	1-20	4-29
Extremes height	2-5	.5-1.5	.5-1.5	.25-2
Average depth blind	7.5	3	3.9	14+
Extremes depth blind	3.5-18	3	3.5	14—?
Per cent blind	90	17	44	17
Per cent anastomosing**	10	83	66	85
Per cent horizontal	50	67	56	50
Per cent vertical or sloped	50	33	44	50
Per cent exfoliated	20	50	11	25
Per cent fractured	50	50	55	75
Per cent weathered	30	—	44	—
Per cent mossy	20	33	39	17
Per cent used 1 year	40	50	100	100
Per cent used 2 years	20	50	77	75
Per cent used 3 years***	40	—	—	—
Average depth, in. egg deposition	7.7	2.6	—	—
Extreme egg deposition	3.5-18	1.5	—	—

* All measurements are given in inches.

** Depth not measurable, interconnecting with multiple deep fractures.

*** Data collected for Highlands only.

Certain invertebrates are frequently found associated with *A. aeneus* on or about the rock outcrops. Often encountered was the slug, *Philomycus carolinensis*, which would enter breeding crevices, eliciting no observed response from the salamander. Associated with moist areas on the rocks were various species of snails. The largest and most prominent form observed was *Mesodon albolabris*. Wherever there existed sufficient soil or surface litter on the rocks to retain some moisture, *Lygidium longicaudatum*, a small isopod, was

TABLE 2.—Daily temperature extremes (°F.) of the habitat of *A. aeneus* for the period June 8-21, 1950 in the Highlands, N. C. region

Location	Highlands Study Area Near Crevice	In Crevice	Diff.	Highlands Weather Station	Diff.
	A	B	A-B	C	C-A
Maximum	69.5	64.2	5.3	73.5	4.0
Minimum	59.6	58.3	1.3	59.5	—0.1
Extremes	75-51	68-54		81-47	



Fig. 4.—One of the more exposed outcrops containing a hibernation crevice (upper left) and a transitory crevice (lower left) on the South Satulah Area. Note that the two crevices are shaded by the overhanging rock ledges. This is an essential feature of exposed outcrops or cliffs where vegetation provides little or no protection against insolation.

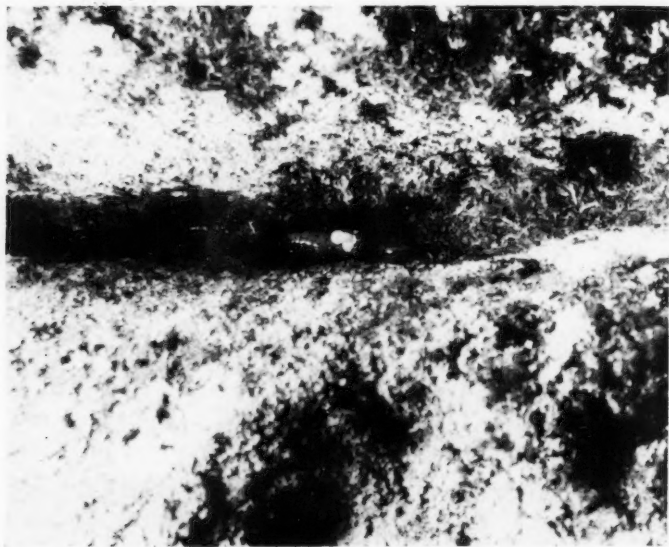


Fig. 5.—An undisturbed female laying eggs. Note the inverted position of the body and the adherence of the eggs to the ceiling of the crevice and to each other. The clutch consisted of twenty-one eggs at completion of laying, and required more than thirty hours to be laid. The eggs and female are four inches from the mouth of the crevice.

to be found. Diplopods were well represented in the areas, and were found frequently in crevices. Due to their gas-releasing mechanism these organisms might have a greater influence on *A. aeneus* in small, blind crevices than one might suspect. *Cherokia georgiana* was by far the most common diplopod occupying the surface litter throughout the study areas.

The spider *Hypochilus thorellii* occurred wherever *A. aeneus* was found in the southern Blue Ridge Mountains, and, judging by the abundance of its distinctive web, it may be said to be one of the most common animals in the area. On the dryer outcrops a thysanurid, *Machilis* sp., was fairly abundant. The cave or camel cricket, *Ceuthophilus* sp., was observed at all localities visited. Crane flies of an undetermined species were found commonly during the summer months beneath damp over-hanging ledges. During the winter of 1949, wasps of the genus *Polistes* were seen hibernating in the exposed crevices of the South Satulah Area. A number of ground beetles, Carabidae, (genus *Scaphinotus*, subgenus *Steniridia*), are of common occurrence in the crevices. A nocturnally active member of the *Agonum reflexa* complex was very abundant on the outcrops. Despite the intense insolation which the "nigger

head" lichen receives in its typical habitat on the outcrops, its thalli harbor by day many of the nocturnal organisms mentioned above.

Vertebrates observed in the area included *Diadophis punctatus edwardsii*, *Plethodon jordani melaventrus* and *Desmognathus ochrophaeus carolinensis*. The snake was observed in the dryer crevices above the Highlands Study Area. Barbour (1950) found that over 50 per cent by volume of the food items in 18 *Diadophis* from Big Black Mountain, Harlan County, Kentucky, was composed of adult and larval salamanders of the genera *Desmognathus* and *Plethodon*. In two of the eighteen snakes, the eggs of *Aneides aeneus* comprised 7.5 per cent of the volume of food present. Therefore, *Diadophis* may be an important predator of *Aneides aeneus*. *Plethodon jordani melaventrus* could be found in the larger crevices of both study areas. *Desmognathus ochrophaeus carolinensis* was noted in wet crevices at all *A. aeneus* localities. In Tallulah Gorge (Georgia), *Eurycea longicauda guttolineata* was captured twice from crevices containing *A. aeneus*. Occasional nests of the phoebe, *Sayornis phoebe*, were encountered. The cloudland deer mouse, *Peromyscus maniculatus nubertriae*, and the red-backed vole, *Clethrionomys gapperi carolinensis*, are the two most abundant small mammals in the ravine habitat of the Highlands region (Odum, 1949). Since the latter species appears to use rock crevices, rather than construct burrows of its own, it may be an important predator on *A. aeneus*.

Life history and annual cycle.—To facilitate presentation, the annual cycle may be divided into four subheads, (1) breeding period, late May to late September, (2) dispersal and aggregation, late September to November, (3) hibernation, November through late April, and (4) post-hibernation aggregation and dispersal, late April to late May.

(1) Breeding period. Prior to mating, no special movements of adults of either sex was noted by the author. Data are inconclusive, but the males appear to enter the breeding crevices and await the appearance of the females. Males are found in May and early June with inflamed and swollen vents. No females marked in the breeding season of 1949 were found in 1950, so it is not known whether females return to the same crevice for egg deposition each year. However, female toe clipped 3-6, which was seen and marked after the breeding season (October 9, 1949) in crevice 15#2 (see Table 3A), deposited eggs in the same crevice in June 1950. Marked females captured in late May could be found with eggs in June in the same or adjacent crevices (Females 7, 1-12 and 3-6, Tables 3A and B). Males tend to wander more than females, but prior to breeding remain in or near the crevice in which they are first encountered.

Both sexes of *Aneides aeneus* are active primarily at night. Light rains were observed to stimulate movement at night, and to a lesser extent in the daytime. Specimens were noted to move about in the daytime in dark portions of large cave or tunnel-like cavities.

Mating occurs in late May or early June. It is not known whether a male

TABLE 3A.—History of individual *Anides aeneus* marked in 1949 on the Highlands Study Area

Sex and individual	Crevice captured	Date marked, 1949	No. of times recaptured, 1949	Last date recaptured, 1949	Subsequent crevices occupied with date	Distance moved in feet	No. of times recaptured, 1950	Crevices and date	Distance moved since last 1949 capture
♂ 1	2#1	5-15	2	8-26	None	0	1	2#2 (6-10)	2
♂ 2	2#1	5-15	1	10-9	None	0	1	2#1 (5-20)	0
♂ 3	14#1	6-14	2	6-27	7-2 (6-27)	5	1	7#2 (6-21)	0
♂ 4	14#1	6-19	1	7-20	7-2 (7-20)	5	0
♂ 5	7#2	8-22	1	10-9	None	0	0	15#5 (6-7)	..
♂ 6-7	15#5	10-9	0	4	15#3 (6-15)	3
								15#1 (6-17)	
♀ 6	15#2	6-12	*	11-20	None	0	2	15#2 (4-16)	0
♀ 7	7#1	6-6	*	9-8	None	0	0
♀ 8	2#1	6-6	*	9-5	None	0	0
♀ 10	2#2	6-11	*	10-9	None	0	0
♀ 11	16#1	6-6	*	9-8	None	0	0
♀ 3-6	15#2	10-9	0	*	15#2 (6-7 & 6-25)	0
♀ 4-5	16#1	10-9	0	1	16#1 (5-20)	0
I**14	15#8	10-9	0	1	15#8 (6-7)	8
I 5-7	15#7	10-9	0	1	RF#2 (6-13)	350

* Guarding eggs continuously between first and last dates given.

** Indicates immature or subadult specimen.

mates with one or more females during the breeding season. Single pairs of salamanders were observed to occupy a crevice together prior to egg laying. Two successive periods of observations during the breeding season failed to reveal if courtship with subsequent clasping is carried on within the crevice. Brooks (1948) reports finding a clasping pair on a cliff face, stating that the individuals were in the normal position for plethodontid salamanders. He observed, "constant movement on the part of both individuals, with body undulations and shifting of mouthholds." In an effort to obtain mating under natural conditions, female 1-3 was placed with male 1-6 in crevice 2#2. After several hours, the male was noted pressing his cheek against the snout of the female. Observations one hour later revealed no change in position. After three hours they were separated, each occupying opposite sides of the crevice. The following morning the female was found dead on a ledge beneath the crevice. Spermatophores obtained from freshly killed males collected June 11, 1950, at Granite City, Jackson County, North Carolina, consisted of an amorphous globule of clear, gelatinous material capped by a whitish mass of active sperm.

Egg laying was noted to have occurred prior to June 6 and was completed by June 16 on the Highlands Study Area in 1949. The process was completed by June 14, 1949, on the South Satulah Area. In 1950 egg laying appeared to be more sporadic on the two areas. Completed clutches were noted on June 7 and a specimen was observed laying on June 20 in the Highlands Study Area. Clutches were noted to have been laid by June 8 on the South Satulah Area and a gravid female was observed on June 21. Courtship and egg laying apparently do not occur simultaneously over the whole region. Gravid females were collected from Tallulah Gorge on July 6, 1950. No females were found to be laying nor were any eggs noted in crevices at this time.

As shown in figure 5, a photograph of an undisturbed female laying eggs in crevice 7#1, eggs are laid while the female lies on her back with her ventral surface pressed close to the ceiling of the crevice. Prior to the appearance of the first egg, and after the female has assumed the inverted position, a small globule of clear, mucoid, adhesive material appears at the lips of the cloaca. This is pressed to the ceiling and becomes one of several cables by which the eggs hang from the ceiling. Each egg is preceded by a small drop of apparently the same material. On removing eggs from a dead female by massage, this material was found to be very adhesive. The drop serves to attach the egg to the original, small globule, and to other eggs. The cable is apparently formed by the weight of the egg pulling against the original globule. The following, extracted from field notes of June 12, 1949, serves to indicate the activity:

12:15 P.M. Female still inverted—posterior portion of the body greatly swollen. Cloaca closely pressed to ceiling of crevice with some transparent fluid noticeable at the point of contact.

3:30 P.M. First egg apparent. She has changed position so as to allow more room between her body and the ceiling—about one eighth of an inch.

I 5-7 15#7 10-9 0 1 (6-7) RF#2 (6-13) 8 350
* Guarding eggs continuously between first and last dates given.
** Indicates immature or subadult specimen.

TABLE 3B.—History of individual *Anides aeneus* marked in 1950 on The Highlands Study Area

Sex and indi-vidual	Crevice cap-tured	Date marked	No. of times recap-tured	Last date recap-tured	Subsequent crevices occupied and dates	Approximate distance recovered from re-lease site in feet
♂ 1-6	2#2	6-9	5	6-19	2#1 (6-19)	6
♂ 1-8	15#8	5-20	1	6-10	15#4 (6-10)	2
♂ 1-11	7#2	5-20	1	6-7	7#2 (6-7)	2
♂ 2-3	15#6	4-16	6	6-25	15#3 (6-17 & 6-20) 15#6 (6-21) 15#7 (6-25)	2
♂ 5-10	14#3	5-26	1	6-14	2#1 (6-14) RF#1 (6-8)	250
♂ 8-13	2#1	5-20	4	6-20	RF#2 (6-14)	300
♀ 1-3	15#1	5-20	2	6-10	None	...
♀ 1-5	15#9	5-20	1	6-10	16#2 (6-10)	12
♀ 1-10	16#1	6-9	1	6-10	None	...
♀ 1-12	7#1	5-20	5	6-14	(6-7 & 6-9) 7#2 (6-13 & 6-14)	2
I* 2-5	2#1	6-19	4	6-21	2#1 (6-19 & 6-21)	0

* Indicates immature or subadult specimen.

Two females were observed throughout the process of oviposition. In one case more than 15 eggs were laid in twenty-seven and one half hours. In another, 15 eggs were laid in twenty-three hours. A third female, after laying five eggs, was observed to remain in laying position for thirty more hours before the process was complete. A single egg from its appearance in the cloaca until its attachment to the ceiling of the crevice required one and one half hours. Another female required nine hours to lay her first egg.

As eggs are laid, the cloaca is shifted from side to side, so that a cluster of eggs results. In exfoliated breeding crevices, the eggs, due to the physical space available between female and rock, may be laid each attached to the rock so as to form a flattened group. In several cases, single eggs were deposited several inches away from the main clutch. Not all eggs remain attached to the rock. In narrow crevices wherein the salamanders were quite active, eggs were observed to fall to the floor and in many cases these were lost from the crevice later on.

The egg is whitish-yellow when first deposited, the color being due to the yolk present. They readily become discolored, darkening considerably during the first week. There is only a slight tendency for the eggs to absorb water after they are laid. The average diameter (including the outer egg membrane) of sixty-two freshly laid eggs was 4.5 mm. Twenty-two clutches of eggs were observed to be deposited at an average depth of 6.3 inches. Only one clutch was deposited at a depth less than 3 inches (1 inch), and several were visible a depth of 18 inches. The number of eggs averaged 17 per clutch (extremes 10 and 26). The above figures are from clutches collected on the two study areas and at Granite City, North Carolina. Table 1 gives a comparison of the average depth of egg deposition on the two study areas.

After laying the eggs, the female turns over and lies to either side or coils around the clutch of eggs. This is considered the guarding period and is known to occur in the life cycle of a number of different salamanders. All marked females, removed from the crevice for identification were observed to return to the crevice and eggs when released several inches away. In many hours of observation in both day and night, the author never found the eggs unguarded unless the female had permanently deserted the crevice. However, in one case, that of crevice 7#2, female 1-12, after an absence of two days the female returned for two days, and then was not seen again. The eggs, if left unguarded or deserted, either disappear all at once or several at a time. Ten eggs were reduced to four after 31 days without the protection of the female. A growth of mold on the eggs was observed after 26 days. Guarding by *A. aeneus* is no passive action. Aggressive lunges and bites are made at objects inserted into the crevice. Until the female apparently became accustomed to the beam of a flashlight and to the insertion of objects into the crevice considerable agitation on the part of the female is observed. One female promptly consumed a small beetle (*Agonum*), as well as several thysanurids when these were placed in a breeding crevice. The presence of other individuals of *A. aeneus*, male, female or immature (naturally occurring or introduced in the crevice) elicits no response from the female. In several cases two females

TABLE 3C.—Summary of Tables 3A and B*

	Total	Number recap- tured same season	Number station- ary	Number moved	Maximum distance recovered feet	Number recap- tured 1950	Number station- ary	Number moved	Maximum distance recovered feet
Males marked 1949.....	6	5	1	2	5	4	2	2	2
Females marked 1949.....	7	5	5	0	..	3	3	0	..
Immatures marked 1949.....	2	0	0	2	0	2	350
Males marked 1950.....	6	6	0	6	300
Females marked 1950.....	4	4	2	2	12
Immatures marked 1950.....	1	1	1	0

* Individuals marked, but never recaptured, are not included in Tables A, B or C. This group includes: 1949, 2 males, 1 female, 3 immature individuals; 1950, 1 male, 3 females, 1 immature individual.

with egg clutches were found within several inches of each other in the same crevice.

The females were negatively phototropic in the majority of cases and would back into the deepest portion of the crevice possible when the crevice was illuminated by the beam of a flashlight. This was also true of males, immature and young individuals. The young, however, would reappear in a matter of minutes if the light was removed.

During the guarding phase, the males and immature individuals are less sedentary than females although some males remained in or near the crevice where first found as shown in Tables 3A and B. Visits to the Highlands Study Area were made at all hours of the night, yet no individuals were found crawling on the trees or over the surface of the ground. However, salamanders did tranverse considerable distances between habitable rock outcrops. Marked specimens 5-10, and 8-13 (see Table 3B) moved 250 feet over periods of 19 and 26 days, respectively. Immature specimen 5-7 moved 350 feet during a period of nine months (Table 3A).

The males often became quite irritated when attempts were made to remove them from the crevices. In such cases they would occasionally snap at an inserted object, but more often they would retreat to the deepest portion of the crevice. The majority of *A. aeneus* were observed with their heads facing the crevice opening or partially protruding from the opening. If a wire was passed behind them, and the specimens touched on the tail, or hind feet, they would move out of the crevice, and were easily picked up.

No defense of territory, nor of any particular crevice, by males was noted. Two males were found together on several occasions at several different localities. As many as eleven specimens (adults and immature individuals) were found in the same crevice at one time.

Aneides aeneus is very agile. Specimens, on being removed from a crevice, would frequently jump six to ten inches and could break a fall by use of a single foot. Individuals were observed to crawl upside down on rough stone in several of the cave-like rock formations visited. The tail, while not prehensile in the full sense of the word, can support the organism and is a definite aid in climbing from crevice to crevice. When the salamander is irritated the tail is thrashed about wildly. As is the case with many of the Caudata, attempted capture by pulling on the tail often results in its separation from the body. Reduction of total tail length in males (prior to, or during the breeding season) might lead to the loss of a potential breeder to the population, since most plethodontid salamanders use the tail in courtship and mating (Noble and Brady, 1930; Stebbins, 1949a).

The entire development of this genus is intraovial, no aquatic larval stages occurring. Several obvious developmental stages and reactions were observed *in situ*. A well-defined headfold and eye was observed on the forty-third day of development. The general body contours as well as the gills were apparent on the fiftieth day, but no macroscopic pigmentation could be seen. At this time the larva was very active and very sensitive to light. There was much twisting and turning within the capsule when the light was shone on the

clutch. The larvae showed evidence of pigmentation on the fifty-fifth day. The coloration of the gills was reddish. About two weeks prior to hatching time the gills begin to diminish in size.

Hatching of the eggs occurred between September 5 and 8, 1949, at the two study areas. Five clutches on the Highlands Study Area, which had been under observation from the time first laid to hatching, required an average incubation prior of 86 days and 19 hours (extremes 84 and 91 days). At hatching there appears to be a breakdown of the egg membranes, and the young salamander forces his head through to the outside. He then gradually undulates his way out of the egg. In coloration and form, the young *Aneides* resembles a diminutive adult. The opercular fold and abdominal cleft through which the gills and yolk sac had previously protruded are not completely closed. Two groups of young whose development and hatching had been observed, were collected and measured. The first, consisting of nine individuals from the Highlands Study Area, averaged 19.7 mm. for the total length (extremes 18.5 to 20.5) and 12.9 mm. for the body length (extremes 12.5 to 13.5). The width of the head averaged 3.5 mm. The second group, composed of 19 individuals from the South Satulah Area, had an average total length of 20.3 mm. (extremes 18.5 to 23) and a body length average of 13.2 mm. (extremes 12.5 to 15). The width of the head averaged 3.5 mm.

Walker and Goodpaster (1941) collecting in Adams County, Ohio, on September 30, 1939, found two groups of young in company with adult females. One group of thirteen ranged from 22 to 24.8 mm. (mean 23.7) in total length; a second group of seventeen young varied from 21.5 to 23.5 mm. (mean 22.5). From the measurements given and the fact that they were still with the adult, these young probably hatched within the month of September. Walker and Goodpaster point out the large size of nostrils, "the diameter of which is contained from 1.5 to 2 times in the distance from the nostril to the anterior angle of the eye." The newly hatched individuals from the two study areas show the same proportions.

All eggs laid did not hatch. A total of 106 plus eggs in seven clutches were seen in June on the Highlands Study Area. From these 73 plus individuals or 69 per cent hatched.

The female is apparently quite impassive to the appearance of the young. However, in introduction of a wire into the crevice, the salamander snapped at it in four of seven cases. Where particular females had become accustomed to the author's light and wire during the guarding phase, some renewed interest in the defense of the young was observed.

There was no effort on the part of the female to keep the young within the crevice. Several individuals were found crawling along a small ledge eight inches away from one crevice, twenty-four hours after hatching. Three other young were observed to crawl out of another crevice causing the female no apparent concern. When attempts to remove the young were made by use of a wire, they would dash for the rear of the crevice and seek refuge in tiny cracks. The young salamanders were not very steady and would frequently lose balance. If persistent attempts to remove them were made, the young

would sometimes roll over, fall on their backs and remain there momentarily with legs disstended (a similar observation has been recorded by Netting and Richmond, 1932).

A growth curve cannot be constructed since the number of individuals collected at any one time is insufficient. On May 20, 1950, four young, from the South Satulah Area which the author believes to have hatched the preceding season averaged 28.3 mm. in total length (extremes 27.5 to 29.5) and 16.8 mm. for body length (extremes 16.5 to 17.5). On the same day at the Highlands Study Area, three young which apparently hatched during the same season averaged 25.3 mm. in total length (24.5 to 26.0) and 15.5 mm. for body length. This represents an increase of 5.6 and 2.6 mm. in the total and body length, respectively, for the Highlands Study Area specimens over a period of about eight and one third months. Those of the South Satulah Area showed an increase of 8.0 and 3.6 mm. for the two measurements made over the same period of time. The terms *immature* and *subadult* specimens have no statistical basis and are designations of sexually immature individuals made by the author, based on the general subjective familiarity with the species in the field.

Aneides aeneus was never observed to feed except under experimental conditions. A guarding female was observed to eat insects when introduced into her crevice. Females compared with males, at the end of the long guarding period, were found to be quite thin (no actual weights were recorded). The stomach and small intestines of two females taken during the guarding phase were empty. The large intestines contained some feces, however. The evidence indicates that females do not leave the eggs to search for food and therefore take little or no food during the three months guarding period. A total of twenty-two stomachs of both females and males have been preserved for a future study. Preliminary examination of several of these indicates that insects form the bulk of the foods (Coleoptera and Formicidae, in particular). Bishop (1928) states that *Aneides aeneus* may be maintained in the laboratory on a diet of fruit flies.

(2) Dispersal and Aggregation. The exact length of time the young and female stay together is not known although from observations made in 1949, the young are known to leave the crevice within two months after hatching. In one instance, female 8, crevice 2#1, the female left the crevice several hours after the removal of the single young individual and 2 spoiled eggs. Female 10, crevice 2#2, was found with fourteen young one month after hatching occurred. Since the adult makes no attempt to keep the young in the crevice, the length of time which the female remain in the crevice with the young apparently depends on the activity of the latter. Observations at all localities visited indicate that the young, after dispersal, generally inhabit moss choked crevices and ledges, occasionally occurring in the non-mossy situations. By November 20 only two young were observed on the Highlands Study Area and none were seen on the South Satulah Area.

Considerable movement of adults takes place during the dispersal and aggregation period. Individuals of both sexes, marked during the breeding

season, were noted in crevices used during the breeding season, but in October, ten individuals not previously seen appeared in the crevices on units 14 and 15. The group included males, females and immature individuals. This influx is part of the aggregation, here designated as the pre-hibernation aggregation. Pre-hibernation aggregation occurred on both study areas, but was more marked on the Highlands Study Area than on the South Satulah Area for reasons discussed below.

(3). Hibernation. Subsequent visits made during the period of November through April revealed only four individuals on the Highlands Study Area and twelve on the South Satulah Area. These were seen in deep anastomosing crevices. In an effort to determine the location of the salamanders during this period, an examination of the soil for an average depth of fifteen inches around several outcrops was made. No salamanders of any species were found. Trees with loose bark were examined and rotten logs were torn apart, but, with the exception of a single *Plethodon jordani melaventris*, no salamanders was found in this type of habitat. The author believes, therefore, that hibernation occurs in the deep interconnecting crevices. This belief is based on the occurrence of large numbers of individuals in deep crevices (or adjacent ones) prior to hibernation and the fact that the only specimens noted during the hibernation period were seen in the anastomosing crevices.

The visible occurrence of twelve individuals on the South Satulah Area, while only four were seen on the Highlands Study Area, during this period, is probably correlated with the greater insolation received on the more exposed South Satulah Area. The winter of 1949-50 was an exceptionally mild one, and it is probable that no salamanders would be observed on either area during a normal winter.

(4) Post-hibernation Aggregation and Dispersal. In late April and early May specimens emerge from hibernation and congregate in the anastomosing or adjacent crevices. This was not as marked an occurrence on the South Satulah Area as on the Highlands Study Area. The post-hibernation aggregation on the Highlands Study Area centered, as did that of pre-hibernation, around the deep crevices in units 14 and 15, and is a further indication of the probability of their winter usage. By late May and early June, individuals had dispersed to the crevices of outcrops in units 2 and 9 and on the rock face (see fig. 2), and the breeding period of a new annual cycle begins.

Mention has been made of the less marked occurrence of the pre- and post-hibernation aggregations on the South Satulah Area. This study area, as previously noted, consisted of one large cliff and several small outcrops. The individuals occupying this area are concentrated on the cliff rather than dispersed to smaller outcrops, thus there is no influx of individuals to or from the hibernation site as on the Highlands Study Area.

There are apparently two major outcrops (units 14, 15) on the Highlands Study Area, the crevices of which are used for hibernation. The other outcrops, while containing crevices suitable for use in the breeding period, are not used for hibernation. It is from the anastomosing crevices found on these outcrops that the author believes the majority of unmarked individuals came.

To summarize, where crevices are suitable for both breeding and hiberna-

tion, individuals of *Aneides* may be sedentary. Where crevices, either deep or shallow, are suitable only for breeding, individuals will move from these to the outcrops with deeper crevices in the fall, and return to the breeding crevices in the spring.

Population Dynamics.—Figure 6 indicates graphically the changes in the visible population which occurred on the study areas. These changes revolved around the four periods of the annual cycle previously discussed. During the breeding period little fluctuation in the total visible population occurred, the population remaining relatively stable until hatching in early September. Subsequent dispersal and hibernation reduced the visible population until April. Post-hibernation aggregation with reappearance of the population in April and May then occurred. With the advent of the breeding period the visible population again becomes stable with little fluctuation in numbers or distribution.

Since the immature and subadult individuals are indicated by a dashed line, and the young by a dotted line, the number of adults comprising the total population may be inferred at any time (fig. 6). The sporadic occurrence of both immatures and young of the preceding hatch (as in June) is reflective of their more concealed habitat, that of mossy crevices and ledges.

The fall peak, while a result primarily of newly hatched individuals, is also composed of an influx of adults. Test and Bingham (1948) in censusing a population of *Plethodon cinereus* indicate that a large percentage of the population was beneath the ground and thus unobservable. Their method of removal of specimens from the census area reduced the pressure on the available surface habitat (litter of various sizes, branches, logs, chips of wood and bark, spoken of as cover), and thus on the fourth census a relatively high number of salamanders still occupied the area, occurring for the most part beneath the large covers. They postulated that there was an important difference between large and small covers, and that this lay in the presence of surface openings made by other organisms, "beneath a very much greater proportion of large covers." The surface openings led into tunnels and burrows which served as refuges for large numbers of *P. cinereus*. An analogous situation between the habitat of *P. cinereus* and that of *A. aeneus* exists. The large covers used by the former may be likened to the anastomosing crevices inhabited by the latter. By use of a crowbar at several localities large anastomosing crevices were opened to reveal specimens, especially females with eggs, which had not been visible previously. Censusing of a colony of *A. aeneus* would then be done best at the fall aggregation in October, since this is the period at which the nearest approach to the total population number probably can be made. That is, adults and immature individuals, not visible during the summer (presumably because of their occurrence in the anastomosing crevices) become visible, and at the same time, visible young of the year can be counted.

Sex determinations were compiled for *Aneides aeneus* collected or observed at four localities (Table 4). Determination in the field of 47 marked individuals was made without known error. All specimens determined as females in the fall were found to be gravid when recaptured in the following spring and early summer. Marked females and males, removed from the South Satulah Area to the laboratory at the termination of the study, were found

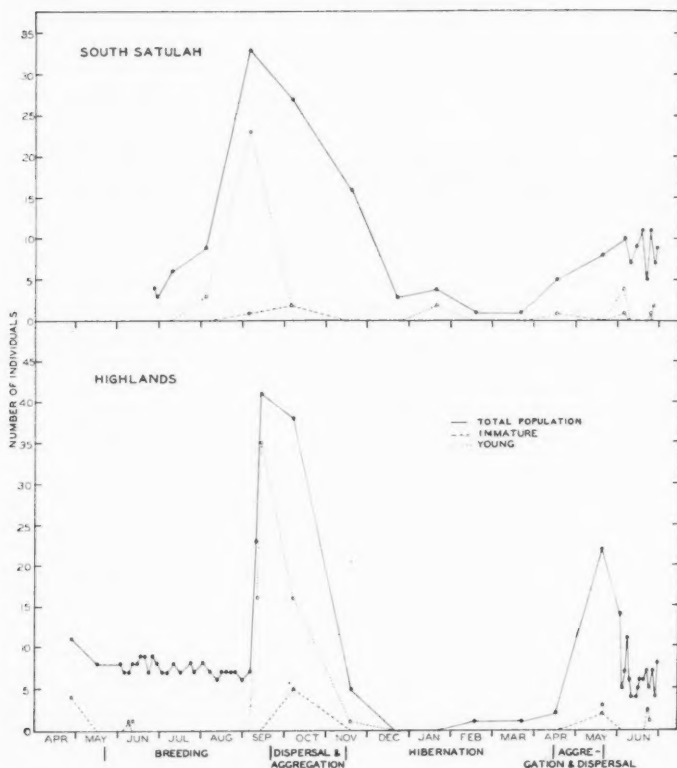


Fig. 6.—Changes in the visible population on the two study areas during an annual cycle and a portion of the next breeding season. See text for further explanation

TABLE 4.—Sex ratios at four localities

Localities	Males	Females
Highlands Study Area	26	17
South Satulah Area	19	17
N. C.: Jackson County, Granite City	17	8
Ga.: Rabun-Habersham counties, Tallulah Gorge	13	5
Total	75	47

to be accurately sexed in the field. Determination of sex was made on as many other individuals as possible by dissection.

When the four samples are tested individually by the chi-square method they show no significant difference from the expected 1 to 1 ratio. When these figures are summed and the chi-square value obtained (6.426), the figure falls well within that considered significantly great. This significant departure from the expected 1 to 1 ratio is probably due to selective collecting based on the habits of the organism. The majority of collections were made at a time when females were guarding eggs and thus not as readily available as males.

PRELIMINARY EXPERIMENTS WITH VITAL LIMITS OF WATER LOSS

Procedure.—During the course of the investigation at the two study areas, *Plethodon jordani melaventris* was seen in the larger crevices of the granite outcrops. Due to its stouter body and less well developed phalanges, lacking terminal expansions, this salamander is prevented from entering the smaller crevices and is unable to climb up to the larger weathered pockets on the outcrops. Chadwick (1940) described the habitat of *P. j. melaventris* (under the name of *Plethodon metcalfi*) in the Highlands region, a short distance from the Highlands Study Area. He reported the examination of about 500 linear feet of subsoil burrows made by other organisms, but used and expanded by *P. j. melaventris*. He found no other vertebrates in the burrows. In the light of Chadwick's findings, the occurrence of *P. j. melaventris* on the rock outcrops was interesting.

Perhaps differences in tolerance to a relatively dry atmosphere (when compared with subsoil burrows) may account for the absence of *P. j. melaventris* from all but a few of the available crevices. Thus, the author desired to compare the ability of adult *Plethodon* and adult *Aneides* to withstand water loss.

Thorson and Svihla (1943) correlated the ability to survive water loss with ecological habitat in ten species of frogs. Littleford, Keller and Phillips (1947) have indicated that the same correlation exists for several plethodontid salamanders.

To obtain this comparative measure of the physiological response and tolerance to drying, a modification of the apparatus used by Hall (1922) was utilized. Air under pressure was passed through a calibrated flow meter, essentially similar to that described by Gilbert and Shive (1941), and into a large moisture absorbing jar containing calcium sulfate (trade name Drierite). From here the moisture free air then passed into a desiccation chamber. The air passed from this latter vessel through two U-tubes, containing calcium sulfate, to the outside. The desiccation chamber, a three-necked distillation flask, was equipped with a thermometer in the center neck, and was floored with a piece of wire screen. This prevented the salamander from coming in contact with the glass and also permitted air to flow freely around the organism at all times.

The temperature was controlled and maintained at 20° C., plus or minus

TABLE 3.—Data on per cent water loss

No. sex	Original weight	Final weight	Weight loss	Water collected	Per cent water loss	Per cent wgt. loss as water	Duration run min.	Liters air/min.	Survived
<i>Plethodon jordani melaventris</i>									
3 ♀	4.942	4.004	.938	.640	12.9	68.6	120	1	Yes
5 ♀	3.024	2.120	.904	.776	25.6	85.8	119	2	No
7 ♂	3.290	2.668	.622	.419	12.7	67.3	74	3	Yes
8 ♂	2.828	1.978	.850	.682	24.1	80.2	91	3	Yes
13* ♂	2.350	1.568	.782				148		No
14* ♂	3.946	2.868	1.078	2.478	22.6	71.8	176	3	Yes
15* ♀	4.656	3.068	1.588				216		No
<i>Aneides aneides</i> , South Satulah									
2 ♂	3.020	2.180	.840	.758	25.0	90.2	120	1	Yes
4 ♀	3.432	2.144	1.288	1.166	33.9	90.5	167	2	Yes
6 ♂	3.590	2.334	1.256	1.014	28.2	80.7	106	3	Yes
9 ♂	2.905	1.898	1.007	.995	34.2	98.9	99	3	Yes
10* ♀	3.029	1.944	1.085				202		Yes
11* ♀	3.660	2.324	1.336	3.252	30.7	80.1	238	3	Yes
12* ♀	3.890	2.322	1.568				228		Yes
<i>Aneides aneides</i> , Tallulah Gorge									
16 ♂	2.896	1.805	1.091	1.085	37.4	99	140	3	Yes
17 ♂	3.170	2.053	1.177	1.004	31.6	90	144	3	No
18 ♂	2.648	1.825	.823	.798	30.1	97	101	3	Yes
19 ♂	2.662	1.898	.764	.547	20.5	72	92	3	Yes
20 ♀	3.304	2.413	.991	.751	22.7	76	106	3	Yes
21 ♂	2.368	1.880	.488	.444	18.7	91	56	3	No
22 Y**	.533	.366	.167	.107	20.0	64	41	3	No
23 Y	.397	.296	.101	.089	22.4	87	34	3	Yes

All weights in the above table are in grams.

* These specimens were run in groups of three.

** Indicates individuals less than one year old.

23 Y
 .397
 .355
 .366
 .167
 .089
 .22.4
 .64
 .41
 .34
 3
 3
 No
 Yes

All weights in the above table are in grams.

* These specimens were run in groups of three.

** Indicates individuals less than one year old.

one degree, by means of a water bath surrounding the desiccation chamber. Calibration of the flow meter was made by use of a wet-test gas meter.

Frequent checks were made to see that all measurable moisture was being absorbed before the entrance of the air into the desiccation chamber. This was accomplished by use of a U-tube of known weight placed in the system between the moisture absorbing jar and the desiccation chamber. The tube was then weighed at the termination of a single run; no measurable moisture was obtained at any time the check was applied.

The salamanders used in these experiments were obtained from Highlands, North Carolina, and transported under refrigeration to the laboratory. A second group of salamanders was collected in Tallulah Gorge, Georgia, and brought into the laboratory without benefit of refrigeration. The salamanders (in the case of all runs made with single specimens in the desiccation chamber) were utilized within forty-eight hours after capture. Littleford, Keller and Phillips (1947) indicated that no significant difference in the results occurred when the salamanders were maintained in moist dishes under refrigeration for forty-eight hours.

A procedure similar to that of Littleford, Keller and Phillips (1947) was followed. Prior to testing, the animal was taken from the refrigerator, washed to remove extraneous material, and all excess surface water blotted from the specimen between paper toweling. It was then weighed on an analytical balance and placed directly into the desiccation chamber. The U-tubes at the end of the system were weighed prior to the beginning of the flow of air. The specimen was watched until approaching death was indicated by the cessation of throat pulsations. The animal was weighed immediately at this point and then placed between wet paper toweling in a Petri dish before being placed in the refrigerator. It was examined after an interval of one hour to determine whether it had survived, and the amount of water regained. The U-tubes were also removed and weighed to determine the amount of moisture lost from the organism. Varying rates of air flow were utilized.

Results.—Table 5 presents the results obtained from the exsiccation of two series of salamanders. The first consisted of seven specimens of each of two species, *Plethodon jordani melaventris* and *Aneides aeneus*, collected at the South Satulah Area. The second lot contained eight *Aneides aeneus* collected from Tallulah Gorge, Georgia.

It may be noted that at equivalent rates of flow, *A. aeneus* is able to withstand the drying longer than *P. jordani melaventris*. All seven specimens of *A. aeneus* survived whereas only four of the *Plethodon* survived. Water loss in *P. j. melaventris* varied from 12.7 to 25.6 per cent of the original weight. The average loss was 18.8 per cent. *Aneides aeneus* from the same locality showed a water loss ranging considerably higher, 25.0 to 34.2 per cent, with an average of 30.4 per cent. Six adult *A. aeneus* from Tallulah Gorge are intermediate, varying from 18.7 to 37.4 per cent with an average of 26.8 per cent. There is little significance in the results of the effect of increase flow of air except on the duration of the run, the data suggesting an inverse rela-

tionship. Noble (1931: 442) states that rapid drying is far more serious than slow drying.

When the data are examined in the cases where three individuals were run together, *A. aeneus* again shows a higher percentage of water lost per original weight, and in general is able to survive exsiccation better than *P. jordani melaventris*. A marked increase in the duration of the run for both species may be noted, with *A. aeneus* averaging 222.6 minutes, while *P. j. melaventris* shows an average of 180 minutes. This increase in duration is probably due to what might be termed "the Allee effect," that is, a group, or aggregation of individuals, may survive adverse environmental conditions better than a single individual (Allee, 1926, 1931). This was more pronounced with *Aneides* than with *Plethodon*, and is in keeping with their observed activity under natural conditions. The former is frequently seen in groups of two or more specimens, whereas the latter is rarely gregarious.

Several interesting reactions were noted during the experiment. In the case of *Plethodon jordani melaventris* what may be termed a "digging response" occurred. The head was bowed and motions of the digging type were made against the screen floor of the chamber. This response was observed in each case, and was more pronounced in the later stages of the experiment. Goldsmith (1926, in Noble, 1931: 415) observed that digging reactions could be induced in the spade foot toad, *Scaphiopus hammondi*, when subjected to evaporation. This organism is somewhat more fossorial than is *Plethodon*. The salamander also wandered over the chamber and made futile attempts at climbing.

Aneides aeneus succeeded in climbing much better than *Plethodon jordani melaventris*, using its tail more effectively. In all cases except one, *Aneides* attempted to climb out of the chamber via the neck containing the outgoing air tube during the first few minutes of the experiment (sometimes repeated at later intervals). Toward the later stages, just before cessation of throat movements, loss of appendage coordination occurred in *P. j. melaventris* and all subsequent movement was essentially a body undulation. In *A. aeneus* little impairment of appendage coordination was apparent.

The results in general indicate that *Aneides aeneus* has the ability to live in a habitat presenting definite physiological barriers (as well as the previously pointed out morphological ones) to *P. j. melaventris*, and thus is able to escape space competition with the latter species.

DISCUSSION

It is only when one wishes to make a comparison with other species that that paucity of life history data about Plethodontidae is realized. It is seen that *Aneides aeneus* retains the habit of turning upside down during egg deposition. This has been noted to occur in a number of aquatic species and in several of the more terrestrial forms, *Plethodon c. cinereus* and *Desmognathus o. ochrophaeus*. Pope (1928) compared the manner of attachment of the eggs to the ceiling of the brooding cavity by *Aneides l. lugubris* with that of *A. aeneus*. He noted that eggs of the latter were directly adherent to

one another, and that the entire cluster was attached to the ceiling of the cavity by one or more short cables. *Aneides l. lugubris* attaches its eggs separately, each by its own cable. As indicated above, *A. aeneus* occasionally lays its eggs separately where the space between the ceiling and floor of the cavity is a limiting factor. In these cases, the eggs are attached by a small amount of mucoid material, normally serving to adhere the egg to the cluster or to one of the several cables by which the cluster is suspended. There is apparently no difference in the mode of life history, as far as it was reported by Pope (1928), in the arboreal habitat and as observed by the author in the rock habitat.

Noble (1931: 413, and others) have indicated that the presence of the female salamander in company with the eggs may prevent the growth of mold upon them by virtue of her dermal secretions. During this investigation, eggs accompanied by females were never invaded by mold. In the only case where eggs were deserted, and yet remained in the crevice for some time (31 days), mold was observed to develop on them.

The eggs of *A. aeneus* are apparently the smallest of any found in the genus *Aneides* (at this time data on breeding and egg size are only incompletely known for *A. flavipunctatus*, *A. ferreus*, *A. hardii* and *A. l. lugubris*). The breeding period is approximately the same for *A. aeneus* and the other known *Aneides* species.

The question whether or not *Aneides* exhibits any true territorial behavior (i.e. whether males defend an area or crevice against other males of the same species) still remains to be answered. No evidence of territorialism was found. Very few observations were made before pairing in May, and it is possible that territorial defense might occur for a brief period at that time.

The two periods which, because of the lack of time, received the least study, and yet are important in the annual cycle, are pre-pairing and pairing in May, and pre-hibernation in October and November. Further study at these times would probably answer many questions.

No attempts to study geographic variation in *Aneides aeneus* were made in this investigation. When specimens from Tallulah Gorge in Georgia are compared with material from Highlands, North Carolina, it is obvious that there is a greater concentration of pigment on the dorsal surface of the head and more intense coloration of the dorsal surface in general in the former. The sedentary nature of the organism together with its specific habitat requirements point to a localized distribution over its range, probably with little gene interchange between colonies. Thus a study of geographic variation should be made.

Lowe (1950) has indicated that the range of *Aneides aeneus* is limited to the eastern sector of the former transcontinental tertiary temperate forest, the Arcto-Tertiary Flora of Chaney, Condit and Axelrod (1944). The Arcto-Tertiary Flora of the eastern United States was composed primarily of broad-leaved deciduous genera, conifers being of minor importance (Chaney, Condit and Axelrod, 1944). Braun (1941) refers to the relatively unchanged

descendant of this Flora as the mixed mesophytic forest, which is preserved in its least differentiated condition in the Cumberland Mountains and Appalachian Plateaus province. Peripherally, this mixed mesophytic forest differentiates into its three segregants (association-segregates) generally recognized by ecologists as: (1) beech-maple to the north, (2) oak-chestnut to the southeast, and (3) oak-hickory to the southwest. Small stands of the relatively undifferentiated mixed mesophytic forest, however, are able to maintain themselves under special microclimatic conditions outside the area where it is typically developed (Braun, 1941; Cain, 1943). The occurrence of *A. aeneus* in an arboreal, or arboreal-rock, habitat appears to coincide with the optimal development of the mixed mesophytic forest (see fig. 1). Outside of the regions where the mixed mesophytic forest is typically developed, *A. aeneus* seems to live only in rock crevices in close association with small isolated stands of mixed mesophytic forest existing there under special microclimatic conditions.

Lowe (1950) suggests the disjunction of a transcontinental distribution of *Aneides* during the Miocene, thus segregating the eastern and western forms, a hypothesis with which this author is in complete agreement. He further points out the association of the genus *Aneides* with various segregates of the Arcto-Tertiary Flora. The habitat of at least two of the western components of the genus, *A. ferreus* and *A. l. lugubris*, is arboreal. The former, regarded as more closely related to *A. aeneus*, is also more arboreal than *A. l. lugubris* (Myers and Maslin, 1948). Thus, when one considers the occurrence of the most primitive member of the genus, *A. aeneus*, in trees in a region apparently similar to the original transcontinental habitat, together with the arboreal habits of two disjunct species, one of which is closely related to *A. aeneus*, the hypothesis that the arboreal habitat was primary and that the occurrence of *Aneides aeneus* in the rock habitat is of secondary derivation may be advanced.

Topographic-climatic changes which have influenced the segregation of the mixed mesophytic forest may have indirectly resulted in the assumption of a rock habitat by *A. aeneus* over a majority of its range. While the author can see no correlation with any particular rock type or formation, the requirements of the organism for certain types of crevices may lead it to follow that formation which best suits its requirements of limited range in temperature and relatively high humidity. Thus its occurrence in shaded sandstone of the Pottsville series wherever this porous, ridge making formation is present is not unexpected (Gentry, personal correspondence, 1949, states, "I have found that its (*A. aeneus*) range adheres very closely to sandstone, especially the Pottsville sandstone. I have also collected it in Alabama following the Pottsville formation nearly to the Mississippi State line."). Braun (1941) points out that the mixed mesophytic forests and the cove hardwoods of the mountains of Tennessee and western North Carolina are similar, indicating the occurrence of the forest in ravine slopes, coves, and in gorges. Cain (1943) expresses the opinion that the cove hardwood forests of the Southern Appalachians are nearly identical with the widespread forests of the Tertiary.

Six localities visited by the author were located in such situations, where shaded igneous rock outcrops and overhanging cliffs provided suitable habitat for the salamander. Indeed, it is probable that further search of the Blue Ridge Mountains in similar habitats from Georgia to Virginia might reveal isolated colonies of *A. aeneus*.

The effects of man's activities, lumbering and clearing of forested areas, may also influence the habitat choice and distribution of this organism. In this regard, N. B. Green (personal correspondence, 1950) states, "on the assumption that *Aneides* must have been here before the Ohio River, I have explored the area immediately west of the river here (Huntington, W. Va.) in Ohio and was able to obtain some specimens from rock crevices in a shallow cave near the Ohio River in Lawrence County. The history of southeastern Ohio is tied in with the scarcity of records, I believe, in this manner: At the close of the last century and earlier, the wooded slopes of southeastern Ohio were cleared of timber to provide fuel for the smelting furnaces. This destroyed the habitat of *Aneides* and only those that were fortunate to find deep rock crevices and caves survived. For this reason its distribution is somewhat spotty."

Another factor which might be responsible for selection of a rock habitat by *Aneides aeneus* is competition. Assuming that the arboreal habitat is the original one, *A. aeneus* being a relic member of its family, may have become adapted to the specialized habitat where it escapes competition with other plethodontid salamanders. In vertebrates there are many examples of relic species which are either ecologically or geographically peripheral. In the Highlands region *Plethodon jordani melaventris* is abundant in logs and in subsoil burrows around the outcrops (as well as in the larger and more easily accessible crevices) in which *Aneides* occurs, and would seem to be a possible competitor. As already indicated, tolerance tests were made between *Aneides* and *Plethodon* to see if there existed any obvious physiological difference which might give either species an advantage. The results, although preliminary, clearly indicated that *Aneides aeneus* is more resistant to drying than *Plethodon jordani melaventris*, and therefore better able to live in relatively dry rock crevices. Morphologically, *Aneides* is better adapted to life in the crevices by virtue of its flatter body and better climbing ability. Therefore, by selecting rock crevices, *Aneides* escapes competition from other salamanders almost entirely. Its niche over a large part of its range is entirely different from that of its closest relatives. This may have been an important factor in the continued survival of this "old" species over a large range. A study of the food habits of *A. aeneus* and *P. j. melaventris* is in progress and may shed further light on this subject.

Thus, it is evident that a knowledge of life history, physiological tolerance and food habits are all necessary before the ecological niche relations and distribution can be understood. Because of its sedentary nature, specialized habitat and abundance in spotty localities over a wide range, *Aneides aeneus* becomes an excellent tool in ecological life history research.

SUMMARY

This study of *Aneides aeneus* consisted of three parts, (1) determination and mapping of the distribution and habitat choice as revealed by the author's observations, literature and correspondence, (2) an investigation of the life history and ecology carried out intensively on two colonies in the vicinity of Highlands, North Carolina, and less intensively at four other localities in Georgia, North Carolina and South Carolina, (3) preliminary water loss tolerance tests in the laboratory.

The distribution of *Aneides aeneus* coincides with the Appalachian Plateau and Blue Ridge physiographic provinces of Fenneman, there being no known occurrence of the species in the Appalachian Valley.

In eastern Kentucky, southwestern Virginia and adjacent portions of Tennessee *Aneides aeneus* is found to occur in an arboreal or arboreal-rock crevice habitat. Its habitat in all other portions of its range is chiefly rock crevices. The region of arboreal habitat coincides with the undifferentiated mixed mesophytic forest of Braun, while the rock habitat generally occurs in regions of segregated forests of the mixed mesophytic type.

Two areas, designated as (1) Highlands Study Area, and (2) South Satulah Area, were visited throughout a complete annual cycle and part of a second breeding season (April 30, 1949 to June 25, 1950). Rock crevices within these two areas were numbered and mapped. Fifty-two individual *Aneides* were marked by toe clipping and observations were made on the salamander population and on associated fauna and flora. During June, 1950, records were kept on temperature and humidity of the two localities.

Data obtained on the crevices containing *Aneides* indicate two general types of crevice, one used for breeding, another used in a transitory manner. The crevices are moist but not wet, and are always shaded for the major portion of the day. Average daily maximum and minimum temperatures within the crevice were 5.3° F. and 1.3° F. respectively lower than those prevailing in the general area (within eight feet of the crevice) during the period June 8 to June 21, 1950. Relative humidity for the same period averaged 99.1 maximum and 75.3 minimum, with extremes of 100 and 61. This climatic picture is characteristic of the Highlands Plateau and adjacent montane areas.

The annual cycle of *Aneides aeneus* was found to consist of four periods: (1) the breeding period, (2) the dispersal and aggregation period, (3) the hibernation period, (4) the post-hibernation aggregation and dispersal period.

The breeding period, late May to late September, includes mating, egg laying and hatching. Egg laying was noted to have occurred prior to June 6 and to have been completed by June 14, 1949 on both study areas. In 1950, it was not completed by June 21 on either study area. Three females required 23, 27.5 and 30 hours to complete laying. The eggs typically form a cluster hanging from the ceiling of the crevice by several cables, but in some cases they are laid as a flattened mass. The color of the freshly laid eggs is whitish-yellow and they have an average diameter of 4.5 mm. for the 62 eggs measured. The number of eggs varied from 10 to 26 (mean 17) per clutch in

22 clutches examined. The eggs are guarded by the female at all times, and the guarding period varies, depending on the activity of the newly hatched young. Intraovular development required an average of 86 days and 19 hours from laying to hatching (extremes 84 to 91 days) for five clutches observed. Twenty-eight newly hatched young from both study areas varied in total length from 18.5 to 23.0 mm. (mean 20.0) and in body length from 12.5 to 15 mm. (mean 13.1).

The dispersal and aggregation period occurs from late September to November. The young and adult females leave the breeding crevices in most cases during this period. The young apparently choose moss filled crevices and ledges in which they are well concealed. The adults begin to gather in the vicinity of deep interconnecting crevices during October. It is believed that *Aneides aeneus* spends the winter in this type crevice. This assembling of individuals is spoken of as the pre-hibernation aggregation.

Hibernation occurs from November through late April. On the evidence that individuals were more concentrated in deep anastomosing crevices, it is concluded that crevices of this type serve for hibernation purposes. No individuals were found beneath the soil surface or in rotten logs.

Post-hibernation aggregation and dispersal occurs in late April and early May when the salamanders reappear and congregate in the vicinity of the "hibernation" crevices. Dispersal to the outlying breeding crevices takes place early in June. Where crevices are utilized for both breeding and "hibernation," *Aneides* may be sedentary.

Since the greater portion of the non-hibernation cycle is spent by the female in egg laying and guarding of the young, they are naturally more sedentary than the male and immature salamanders. Both sexes are more active at night. Males generally remain in or near the crevices where first found, but marked individuals were noted to move as much as 300 feet.

Changes in the visible population on the two study areas are shown graphically in figure 6. Fluctuations in the number of visible individuals and in their distribution throughout the areas are the result of difference in the activity of the organism during the four periods of the annual cycle. The fall peak is due to an influx of individuals around the "hibernation" crevices and is considered as the best time for censusing an *Aneides* population.

Collecting at four localities revealed a significant departure from an expected one to one sex ratio when individuals obtained were tested by the chi-square method. This is believed to be due to selective collecting based on the habits of the species.

Plethodon jordani melaventrus was frequently seen to occupy the larger and more easily accessible crevices, but rarely to occur in the same crevice with *Aneides aeneus*. Preliminary experiments comparing the two species with respect to vital limits of water loss were carried out in the laboratory. These indicate that *A. aeneus* is more capable physiologically to live in the relatively dry crevice habitat than is *P. j. melaventrus*. Morphologically, the former is better adapted for climbing and entering very narrow crevices in the rock. It would seem that *Aneides aeneus* is able to escape direct competition with

P. j. melaventris and other salamanders by selection of its ecologically peripheral niche, and this may be a factor in its continued survival over a large range. The sedentary nature of the species, plus the selection of a more or less specialized habitat, points to a colonial existence over its range, probably with little or no gene flow between colonies. Therefore, a study of geographic variation with this species should be made.

Because of the similarity of the mixed mesophytic forest, in which *Aneides aeneus* is found to lead a semi-arboreal existence, to the transcontinental broad-leaved Tertiary forest (the Arcto-Tertiary Flora of Chaney, Condit and Axelrod), and since two of the western *Aneides* derived from a former transcontinental migrant are arboreal, the hypothesis that the arboreal habitat is primary and the rock habitat is secondary has been suggested.

REFERENCES

- ALLEE, W. C. 1926—Studies in animal aggregations: causes and effects of bunching in land isopods. Jour. Exp. Zool. 45: 255-277.
- 1931—Animal aggregation. A study in general sociology. The University of Chicago Press. ix+431.
- BARBOUR, R. W. 1950—The reptiles of Big Black Mountain, Harlan County, Kentucky. Copeia 1950(2): 100-107.
- BISHOP, S. C. 1928—Notes on some amphibians and reptiles from the southeastern states with description of a new salamander from North Carolina. Jour. Elisha Mitchell Sci. Soc. 43: 153-170.
- 1943—Handbook of salamanders. Ithaca: Comstock Publ. Co.: xiv+555.
- BRAUN, E. L. 1941—The differentiation of the deciduous forests of the eastern United States. Ohio Jour. Sci. 41: 235-241.
- BRIMLEY, C. S. 1927—Some records of amphibians and reptiles from North Carolina. Copeia 162: 10-12.
- 1941—The amphibians and reptiles of North Carolina. Installment No. 15, Carolina Tips (Elon College, N. C.) 4: 2-3.
- BROOKS, MAURICE 1948—Clasping in the salamanders *Aneides* and *Desmognathus*. Copeia 1948(1): 65.
- CAIN, S. A. 1943—The Tertiary character of the cove hardwood forests of the Great Smoky Mountains National Park. Bull. Torrey Bot. Club 70: 213-235.
- CHANEY, R. W., CARLTON CONDIT AND D. I. AXELROD 1944—Pliocene floras of California and Oregon. Publ. Carn. Inst. Wash. 533: vii+407.
- CHADWICK, C. S. 1940—Some notes on the burrows of *Plethodon metcalfi*. Copeia 1940(1): 50.
- COPE, E. D. AND A. S. PACKARD, JR. 1881—The fauna of Nickajack Cave. Amer. Nat. 15: 877-882.
- DUNN, E. R. 1926—The salamanders of the family Plethodontidae. Northampton: Smith College Anniversary Publ.: 1441.
- FENNEMAN, N. M. 1938—Physiography of eastern United States. New York: McGraw-Hill Book Co., Inc. xiii+714.
- FOWLER, J. A. 1947—Record for *Aneides aeneus* in Virginia. Copeia 1947(2): 144.
- GENTRY, GLENN 1941—Herpetological collections from counties in the vicinity of the Obey River drainage of Tennessee. Jour. Tenn. Acad. Sci. 16: 329-332.
- GILBERT, S. G. AND J. W. SHIVE 1941—A direct reading flow meter and its use in the respiratory studies with plants. Soil Sci. 51: 55-57.

- GORDON, R. E. AND R. L. SMITH 1949—Notes on the life history of the salamander *Aneides aeneus*. Copeia 1949(3): 173-175.
- HAIRSTON, N. G. 1949—The local distribution and ecology of the plethodontid salamanders of the Southern Appalachians. Ecol. Monogr. 19: 47-73.
- HALL, F. G. 1922—The vital limits of exsiccation of certain animals. Biol. Bull. 42: 31-51.
- HOLT, E. G. 1924—Additional records for the Alabama herpetological catalogue. Copeia 135: 93-95.
- LITTLEFORD, R. A., W. F. KELLER AND N. E. PHILLIPS 1947—Studies on the vital limits of waterloss in the plethodontid salamanders. Ecology 28: 440-447.
- LOWE, C. H. 1950—The systematic status of the salamander *Plethodon hardii*, with a discussion of the biogeographical problems in *Aneides*. Copeia 1950(3): 92-99.
- MYERS, GEORGE S. AND T. PAUL MASLIN 1948—The California plethodontid salamander, *Aneides flavipunctatus* (Strauch), with description of a new subspecies and notes on other western *Aneides*. Proc. Biol. Soc. Wash. 61: 127-138.
- NETTING, M. G. AND NEIL RICHMOND 1932—The green salamander *Aneides aeneus* in northern West Virginia. Copeia 1932(2): 101-102.
- NOBLE, G. K. 1931—The biology of the amphibia. New York: McGraw-Hill Book Co., Inc. xiii+577.
- AND M. K. BRADY 1930—The courtship of the plethodontid salamanders. Copeia 1930(2): 52-54.
- ODUM, E. P. 1949—Small mammals of the Highlands (North Carolina) Plateau. Jour. Mamm. 30: 179-192.
- PENN, G. H., JR. 1940—Notes on the summer herpetology of DeKalb Co., Alabama. Jour. Tenn. Acad. Sci. 15: 352-355.
- PICKENS, A. L. 1927—Amphibians of upper South Carolina. Copeia 165: 106-110.
- POPE, C. H. 1928—Some plethodontid salamanders from North Carolina and Kentucky, with description of a new race of *Leurognathus*. Amer. Mus. Nov. 306: 1-19.
- RHOADS, S. N. 1895—Contributions to the zoology of Tennessee, No. 1, reptiles and amphibians. Proc. Acad. Nat. Sci. Phila. 47: 376-403.
- STEBBINS, R. C. 1949—Courtship of the plethodontid salamander *Ensatina eschscholtzii*. Copeia 1949(4): 274-281.
- TEST, F. H. AND B. A. BINGHAM 1948—Census of a population of the red-backed salamander (*Plethodon cinereus*). Amer. Midl. Nat. 39: 362-372.
- THORSON, T. AND A. SVIHILA 1943—Correlation of the habits of amphibians with their ability to survive the loss of body water. Ecology 24: 374-381.
- U. S. DEPARTMENT OF AGRICULTURE 1941—Climate and man. (U. S. Dept. Agr. Yearbook). Washington: Government Printing Office. xii+1248 pp.
- WALKER, C. F. AND WOODROW GOODPASTER 1941—The green salamander *Aneides aeneus* in Ohio. Copeia 1941(3): 178.
- WELLER, W. H. 1930a—Notes on *Aneides aeneus* Cope and Packard. Proc. Jun. Soc. Nat. Sci. (Cincinnati) 1: 2.
- 1930b—A preliminary list of the salamanders of the Great Smoky Mountains of North Carolina and Tennessee. Ibid. 2: 21-32.
- WELTER, W. A. AND R. W. BARBOUR 1940—Additions to the herpetofauna of north-eastern Kentucky. Copeia 1940(2): 132.

Vertebrate Fauna of North Carolina Coastal Islands

II. Shackleford Banks¹

William L. Engels

Department of Zoology, University of North Carolina, Chapel Hill

CONTENTS

Introduction	702	Vertebrate fauna	721
Nature of the problem	702	Amphibia	723
Geography and topography of Shackleford Banks	702	Reptilia	725
Vegetation	705	Aves	729
Climate	706	Mammalia	734
Effects of hurricanes on topography and habitats	708	Differentiation within the fauna	735
Recent history	713	Comparison with Ocracoke Island fauna	736
Semi-feral domestic animals	721	Discussion	738
		Summary	739
		References	741

INTRODUCTION

Nature of the problem.—The physiographic peculiarities of the North Carolina "outer banks" offer a good opportunity for investigating principles of distribution of land vertebrates. It was pointed out in the first paper of this series (Engels 1942, pp. 273-275) that these so-called "outer banks" are *off-shore bars*, submarine in origin, and therefore barren on emergence from the sea-bottom, some distance from the coast line. Because of the manner of their origin, their fauna and flora must have been acquired through over-water invasion, as in the case of typical oceanic islands; because of their position, the source of invading species is limited to the adjacent mainland.

Our study has been limited to tetrapod vertebrates, exclusive of the shore- and aquatic birds, and exclusive of birds occurring only as winter visitants or migrants. The primary aim has been, simply, to ascertain which species have become established on the various islands, and which species have been apparently excluded.

*Geography and topography of Shackleford Banks.*²—One of the chain of islands forming the North Carolina "outer banks," Shackleford extends to the westward from Cape Lookout, to about Long. 76° 39' W., at Lat. 34° 41' N. Shackleford Point, at its westward extremity, is not quite 2 miles from

¹ Some of the field work (1939) on which this study is based was aided by a grant from the Smith Research Fund, administered by the Graduate School, University of North Carolina. Acknowledgment is due the director, U. S. Fish and Wildlife Service, for use of the facilities of the Fishery Laboratory, Beaufort, N. C., and to Dr. H. F. Prytherch, formerly director of that laboratory, for many courtesies.

² I was camped on Shackleford Banks 28 days, in all: June 15-July 1, 1939 (Wade Shore); July 20-24, 1940 (High Hill); June 10-15, 1948 (Wade Shore). An additional 33 man-days of collecting are in the record as a result of one-day trips to the island with students in May of 1940, 1941, 1942 and 1946, and March, 1950.

the coastal town of Beaufort, N. C.; at its eastern end it is about 5 miles from the island to the nearest point on the mainland (figs. 1, 5-7). The island is at present separated from Core Banks and Cape Lookout by a narrow cut known as The Drain; to the west, Beaufort Inlet, more than 1-1/3 miles wide, separates it from Bogue Banks. Along the slightly curving length of the island, it is just under 8 miles from Beaufort Inlet to The Drain. Toward

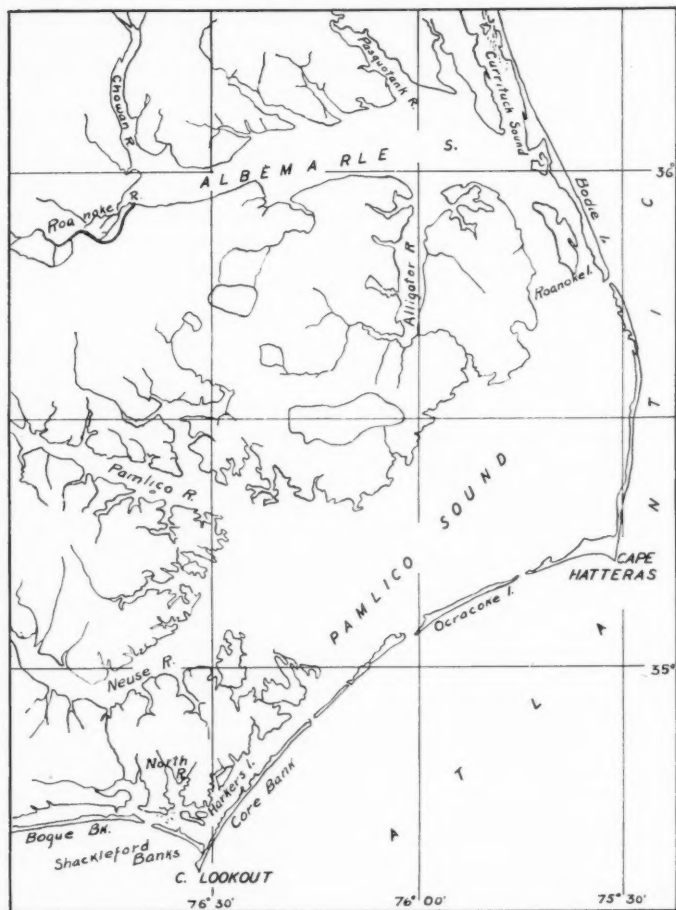


Fig. 1.—The North Carolina "outer banks," and adjacent mainland

each end, the island is about 1100 yards ($\frac{5}{8}$ mile) wide, but through the greater part of its length the width does not exceed 600 yards; in places it is barely 400 yards across the island from ocean to sound.

Between the mainland and the island is Back Sound, which communicates to the northeast with Pamlico, *via* Core, Sound. Back Sound receives the North River, a wide but short tidal creek and estuary coming out of the lowland to the south of the Neuse River.

The tides enter Back Sound, and return to the ocean, through Beaufort Inlet. In the sound, the tidal currents run parallel to the shore of the island; but, towards Shackleford Point, the tide ebbing out of the North River and The Straits (back of Harkers Island) tends to strike against the inner beach.

On the outer, ocean side, a broad beach of sand and broken shell runs the length of the island. On the western third of the island this beach passes directly over into a sandy wasteland extending 300 to 600 yards inland to an irregular but continuous wall of sand from 3 to 20 feet high, which is advancing across the island. Elsewhere, the beach passes over into a somewhat elevated sandy flat just a few feet above the high water level, and thence slopes gradually downward to the water level of the sound. On the soundward, inner side, a sandy beach extends from Shackleford Point to Whale Creek Bay; beyond this, toward The Drain, only an occasional small beach is developed, the shore line being almost entirely marshy.

Sand dunes are scattered irregularly, each standing more or less isolated, behind the ocean beach; most of them are small, but a few reach a height of about 30 feet. Except for dunes, elevations of more than 3.5 feet above high water level are found only on the western third of the island.

In addition to the extensive marshes on the inner shore east of Whale Creek Bay, there are several marshes back of the sandy inner beach between Whale Creek Bay and Shackleford Point. The level of these is below the level of the beach; the tides usually cut a channel, locally called a "gut," through the beach to the marsh. These channels tend to become sanded up and closed, however; in July, 1940, only one of five (at High Hill Glade) was open to the sound.

There are, now, probably no *permanently fresh* water pools on the island. The only large body of water, The Mullet Pond, was relatively recently a bay communicating freely with the sound. The mouth became sanded up, however, and a low upper beach ridge has developed across it. In March, 1950, it was only slightly brackish, the salinity being at that time about 3 parts per thousand (as compared to about 36 parts per thousand, the same day, in the North River). However, this pond is subject, more or less frequently, to flooding with salt water from the sound, as in the great hurricane of 1933 (see below, p. 708); it was flooded also in 1937, and probably again in the early 1940's. Periodically, then, the salinity of The Mullet Pond must rise considerably. On my first visit to the island, in 1939, there was a fairly large fresh water pool, some 30 feet long, back of the western edge of Whale Creek Bay, but this has since become filled up by blow-off from the sand wall. The same fate apparently had already then overtaken the fresh water pools mentioned

by Lewis (1917) in the neighborhood of Diamond City. There are now only a few trough-like pools there, on the grassy flat close by the marshes and beaches of the sound, which must also be frequently flooded with salt water, like the Mullet Pond. In May, 1950, in a typical pool, we found the salinity to be about 5 parts per thousand.

Temporary fresh water pools are quite numerous, however, as one might expect on this relatively flat, sandy terrain, where every slight depression gathers water with each rain. Since the amount of rainfall during almost every month of the year is rather high (see below, p. 708) there is probably always some standing surface water somewhere or another on the island.

At the time of my first visit (1939), there were only two buildings on the island, each a one-room shed, the one just west of The Mullet Pond, the other on Wade Shore. Since then a summer cottage has been built on Wade Shore, and a hunter's camp on the flat east of Whale Creek Bay. There are no permanent residents on the island.

Vegetation.—The vegetation of the island has been described in detail by Lewis (1917).³ At the present time, there is a marked contrast in the aspect of the vegetational cover eastward and westward of Whale Creek Bay. From Whale Creek Bay to The Drain, trees are virtually absent. The sound is bordered by salt marshes in which either *Spartina* or *Salicornia* is dominant; with a rise in soil level of just a few inches, these species give way to the spike-rush (*Juncus*) which often forms dense, closed stands, but is frequently associated with the marsh elder (*Iva*). From the salt marsh toward the open ocean beach is a grassland of *Scirpus*, *Paspalum* and *Spartina patens*. These grasses are all less than knee-high, seldom exceeding 20 inches. Toward the outer third of the island's width, these grasses give way to sea-oats (*Uniola*) relatively sparsely placed. Beyond the sea-oats and the dunes is the barren ocean beach. Standing out conspicuously from this expanse of grassland are

³ Lewis classifies the plant formations on Shackleford Banks as follows:

I. Sand strand vegetation.

1. Treeless (open):

- a. Inner beach formation: *Croton-Cenchrus* association.
- b. Outer beach formation: *Salsola-Euphorbia* association.
- c. Dune formation: *Uniola paniculata* association.

2. Trees and shrubs (closed):

- a. Thicket formation: *Ilex vomitoria* association.
- b. Thicket woodland formation: *Persea-Callicarpa* association.
- c. Woodland formation: *Quercus virginiana* association.

II. Marsh vegetation.

- 1. Salt marsh formation (closed): *Spartina-Salicornia* association.
- 2. Creek marsh formation (closed): *Juncus-Eleocharis* association.
- 3. Dune marsh formation.
 - a. *Cladium-Kosteletzyka* association.
 - b. *Proserpinaca-Aspidium* association.
 - c. *Isnardia-Pluchea* association.
 - d. *Acorus-Salix* association.
- 4. Tidal flat formation (closed): *Scirpus-Paspalum* association.

two small groups of live oaks, growing on small hammocks of sand at the inner edge of the salt marsh (figs. 12 lower, and 13 upper). These are known locally as Sam Winters Lump and Bells Island—each is less than an acre in extent. The land area, from Whale Creek Bay to The Drain, comprises slightly over 2 square miles. Somewhat less than half of this is grassland, and less than $\frac{1}{4}$ salt marsh. The remainder is more or less equally divided between barren sand, and sand sparsely covered with sea-oats.

Westward of Whale Creek Bay the island, as seen from the sound, appears to be well wooded. The dominant elements in this woodland cover are the live oak (*Quercus virginiana*), the red cedar (*Juniperus virginiana*), and the yaupon holly (*Ilex vomitoria*) (fig. 10 lower and 12 upper). Other conspicuous trees, but much fewer in number, are the loblolly pine (*Pinus taeda*), the red bay (*Persea palustris*) and the American holly (*Ilex opaca*).

Red cedars frequently form dense stands, to the exclusion of other forms, especially on the tops of old dunes between Whale Creek Bay and High Hill Glade. In a number of places, the live oaks form an open woodland, with interspersed pine, holly and bay trees. The back slopes of the old dunes are commonly covered with a scattering of low shrubby forms of yaupon holly (fig. 10 lower); elsewhere this holly forms tall, dense and impenetrable thickets.

The woodland is intersected at several points by salt marshes, on which *Spartina glabra* is dominant; one of the largest of these, just west of High Hill and known as High Hill Glade, occupies about 20 acres (fig. 11).

Although it is about $2\frac{1}{2}$ miles from one end of the wooded area to the other, the total area covered by woodland and thicket-woodland does not exceed 200 acres, or approximately $\frac{1}{3}$ square mile. It varies in width from 180 yards, in an open woodland near Wade Shore Gut, to 400 yards, in the thicket-woodland west of High Hill Glade. About 200 to 400 yards from the inner beach, then, lies an irregular but continuous wall of sand, from 3 feet to 20 feet high, which is advancing on the woodland from the ocean beach (fig. 8). This sand wall, through most of its length about 15 feet high, is now (1949) from 330 yards up to 600 yards distant from the ocean beach. The intervening area is absolutely devoid of vegetation, except for the sea-oats on a few small outlying dunes. Scattered about on this wasteland, however, are numerous skeletons of sand-killed red cedars (*Juniperus virginiana*) (fig. 10; cf. below, p. 714).

Climate.—Shackleford Banks, and the Beaufort area in general, has a moderately temperate maritime climate (fig. 2). According to the records of the weather station at Beaufort, for a 28-year period ending in 1930 the highest temperature recorded was 97° F., the lowest was 4° F. (U. S. Weather Bureau, 1933). In January, the average daily temperature range (difference between daily maximum and daily minimum temperatures) is 16.4° F., in July only 12.0° F. The continuously frost-free season averages 269 days in length, more than 8 weeks (27%) longer than at Rockingham (211 days), in the same latitude and with an elevation of only 210 feet, but about 120 miles inland. There is little snowfall, on the average only 1.3" annually,

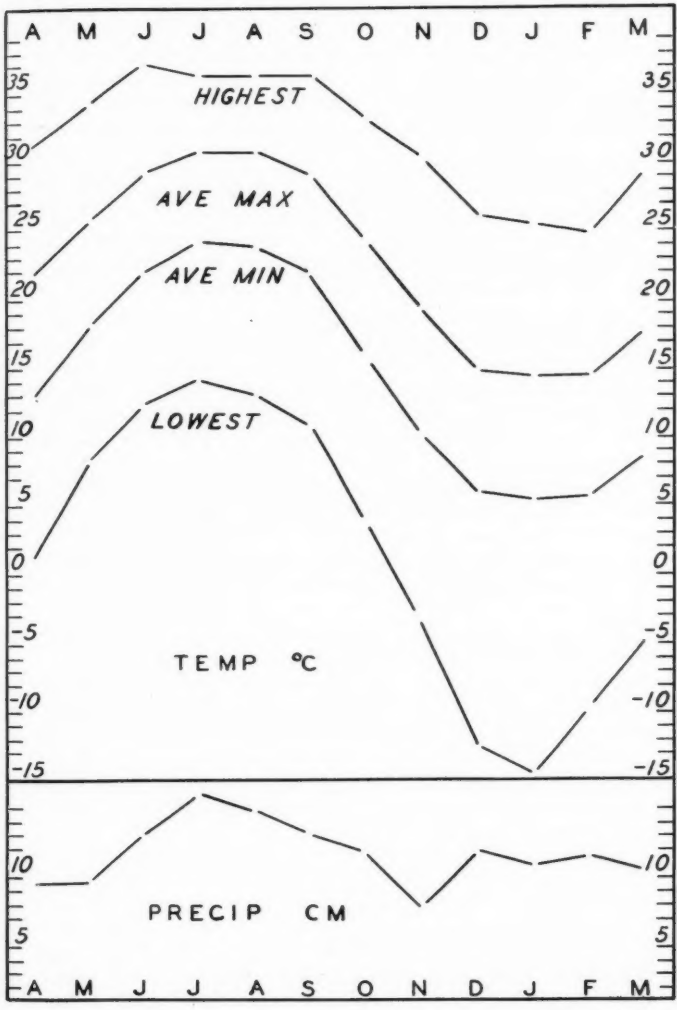


Fig. 2.—Temperature-precipitation chart for Beaufort, N. C.; monthly data, April to March. (Data from U. S. Weather Bureau, 1933.)

more or less evenly distributed from December to March. The rainfall averages 51.46" annually, with a 2.71" falling in the driest month, November. In every month of the year there were, during the period of record, at least 9 days, but not more than 12 days, on which 0.01" or more of precipitation was noted. The prevailing winds, as might be expected, are sea-breezes from the southwest, except in the fall months when they are from the northeast.

Effects of hurricanes on topography and habitats.—The southeastern coast of the United States is well known as a principal target for the Atlantic tropical cyclonic storms called hurricanes. Although no one path is typical of these storms, they commonly move northwestward from their origins in lower latitudes, gaining in intensity as they move; many tend to recurve then as they approach the coast, changing their direction gradually to northeastward.

In this connection, it is important to note that the coast line in the neighborhood of Beaufort runs very nearly in an east-west direction, and that, in general, the southeastern Atlantic coast of the United States lies along a southwest-northeast line, from northern Florida to Cape Hatteras. Indeed, Cape Hatteras is more than 6° of longitude to the eastward of northern Florida. Thus, a considerable expanse of ocean lies to the south and southwest of the North Carolina coast. Hurricanes which recurve in this area of the Atlantic Ocean frequently either pass closely by and roughly parallel to the North Carolina off-shore bars or strike directly over them (fig. 3). It is evident from the data in Tannehill (1944) that the hurricane center passed to the west of the Cape Hatteras station both in November 1904 and in September 1933, and therefore must have struck directly over the off-shore bars somewhere between Shackleford Banks and Ocracoke Island. The center passed just to the east of the Hatteras weather station in 1899, 1924, and 1936, but produced violent winds and seas there in each instance.

The storm of September, 1933, was exceptionally severe in the Beaufort area. According to Tannehill, old residents of Beaufort declared it the worst storm they had ever experienced. I have talked with many of the Harkers Islanders, including ex-Shackleford Bankers, and all agreed that in the fury and persistence of the winds, and in the height and extent of the accompanying flood, it was the most severe storm in their memories. Although the hurricane winds undoubtedly contributed to the consequent changes in the natural landscape, it was the flood water which, in its escape to the ocean, effected the most radical alterations in the topography of Shackleford Banks.

Measurements of the flood waters of this storm are not available, but its height can be approximated by reference to known flood points, such as, for example, the Middle Marshes. These lie between Shackleford Banks and Harkers Island, opposite the mouth of the North River. Their general level is approximately that of mean high water, but they include a few small "lumps" or "hammocks" of sand that rise about 3 feet above the general level, and on these hammocks are a few red cedars, yaupon holly and live oaks, the tallest of which are more than 10 feet in height. All the Harkers Islanders are agreed that the hammocks of the Middle Marshes were covered by the

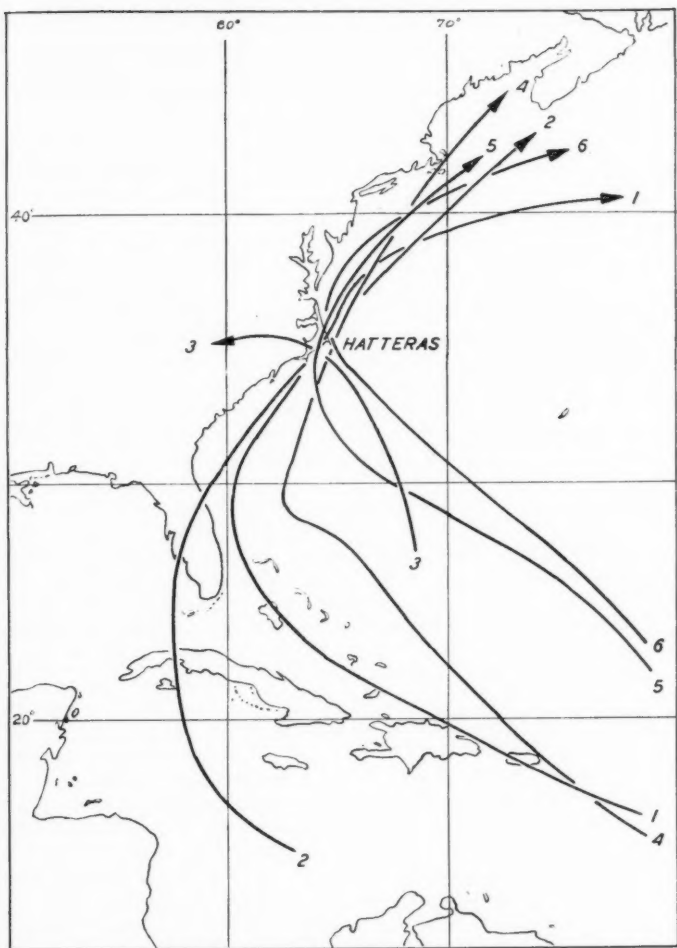


Fig. 3.—Paths of six of the 14 tropical storms of hurricane intensity affecting the North Carolina coast in the period 1899-1943. (Adapted from Tannehill, 1944.) Dates of passage on North Carolina coast: (1) Aug. 16-18, 1899, max. wind 105 m.p.h. N; (2) Nov. 12-13, 1904, max. wind 68 m.p.h. SW; (3) Sept. 2-3, 1913, max. wind 74 m.p.h. SE; (4) Aug. 25-26, 1924, max. wind 74 m.p.h. NW; (5) Sept. 15-16, 1933, max. wind 76 m.p.h. SW; (6) Sept. 18, 1936, max. wind 80 m.p.h. NW. (Wind data recorded at Cape Hatteras; velocity corrected.)

1933 hurricane flood for at least 24 hours; some asserted that not even the tops of the trees were showing. This last is probably an exaggeration; but many of the islanders said that the water stood waist-deep in their front yards, on the south shore of Harkers Island, which would suggest a flood height of at least 5 feet above mean high water.

Tossing in this flood water was the usual debris of wind and flood—boats large and small, the wreckage of buildings, timber, boxes, furniture, trees and logs, and, as one observer put it, “just about everything imaginable.” At that time, Beaufort Inlet provided the only natural passage, from Bogue Banks to Portsmouth Banks, through which this water could escape to the sea. When the storm subsided the impounded flood water broke through the barrier of off-shore bars at numerous points. It cut a new opening, Drum Inlet, through Core Banks, northeastward of Shackleford Banks. (Inlets are misnamed—according to their origin, they should be called “outlets.”) It cut a new opening back of Cape Lookout, The Drain, now separating Shackleford from Core Banks. It broke across Shackleford itself in several places eastward of Whale Creek Bay. These latter cuts were all quickly sanded up on the ocean beach side, but one can see still today where they were gouged out by the flood water and its debris. In walking from Whale Creek Bay to The Drain you will cross several low, narrow troughs, devoid of vegetation, from the bottom of which you can look along, on the one side to the ocean surf without intervening dunes, on the other to the marsh-bordered Sound. Drum Inlet and The Drain remain open, however. In addition to these openings cut through the island, the escaping flood water removed completely the remnant of a scrub-woodland near The Drain, and obliterated the last signs of Diamond City, a village which had been gradually abandoned in the first decade of this century.

Although this hurricane of September, 1933, was extremely violent in its effects on the life and landscape of the Beaufort area, many others have wrought destruction along this coast (fig. 3). The annual hurricane-path maps of Tannehill (1944) for the period 1901-1943 show 13 storms of hurricane intensity on the North Carolina coast; the center of 3 of these moved inland from the Atlantic Ocean on a path more or less normal to the coastline, the others either passed off-shore from southwest to northeast, roughly parallel to the coast, or cut across the Outer Banks from southwest to northeast. (The severe September storm of 1933 was one of the latter.) In a table showing hurricane frequency by states for the 65-year period, 1879-1943, Tannehill lists 16 storms of hurricane intensity for North Carolina's coastline, an average frequency of 1 every 4 years. Two of these, because of their intensity and diameter, were classed among the “great” hurricanes; they were among 21 such reaching the coast of the United States in this period. The first of these two occurred in August 1885; the second, 48 years later, was the violent September storm of 1933.

Finally, we may point out a factor which contributes to the frequency of floods on the North Carolina off-shore bars with their resultant destructive

en the
n; but
yards,
ight of

—boats
es and
” At
Banks
ne sea.
he bar-
Inlet,
re mis-
t cut a
kleford
stward
on the
out by
to The
s, from
an surf
Drum
openings
e rem-
gns of
ne first

t in its
s have
ne-path
hurri-
moved
e coast-
roughly
north-
In a
9-1943,
astline.
their in-
y were
The
er, was

ency of
structive

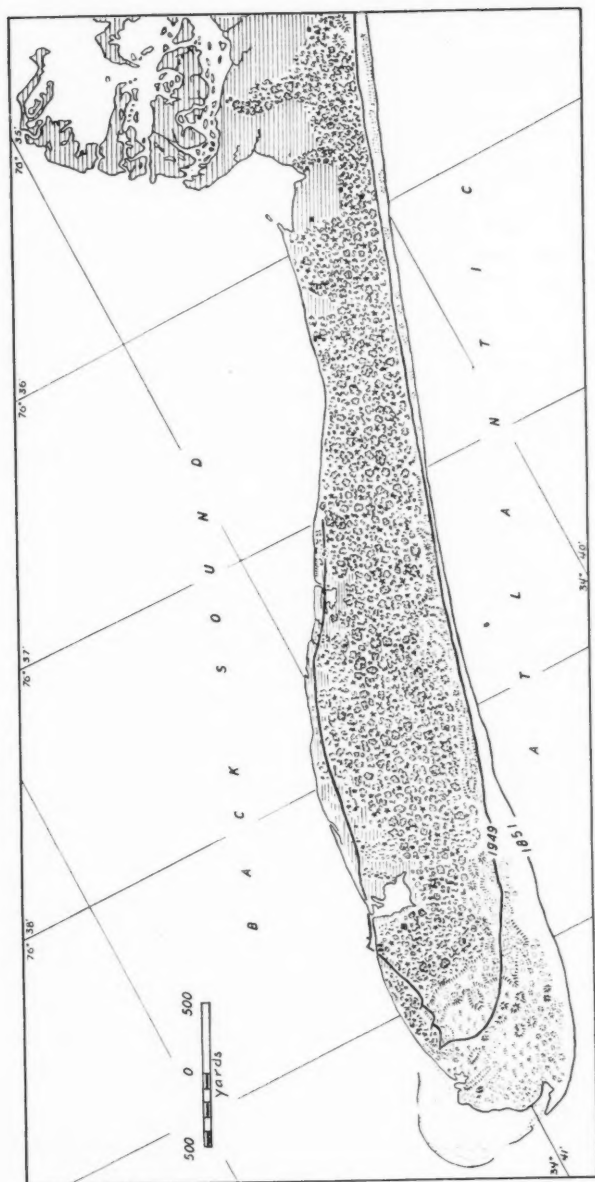


Fig. 4—Western half of Shackelford Banks; topography and vegetation as of 1851; outline as of 1949 superimposed.
(Adapted from U.S.C. and G.S. topographic surveys.)

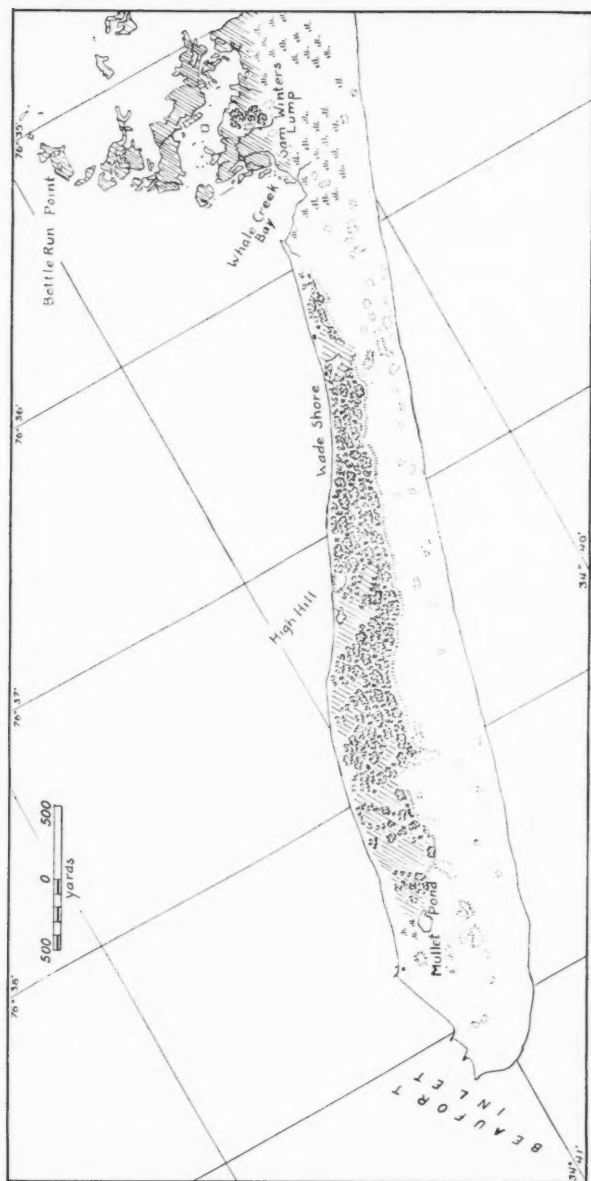


Fig. 5.—Western half of Shackleford Banks, 1949; note great decrease in extent of wooded area as compared to fig. 4; cf. text, pp 713-721 and photographs in figs. 8, 9, and 10. (Adapted from U.S.C. and G.S. topographic surveys.)

effects. According to Tannehill (1944), when a hurricane storm hits in on a coast, if it passes to the right (here, that means to the east) of a place, "the tide is not so high [at that place] and tends to go below the normal as the storm passes the coast line, because the winds [in the left front quadrant of the storm] blow more or less directly off-shore." However, the North Carolina "outer banks" do not form a true coast line but only the outer rim of a series of large lagoons. Hence this effect of Tannehill's "law of storms" is largely nullified here, since the northerly to northwesterly winds of the left front quadrant tend to pile up the waters of Pamlico and Core Sounds behind the banks, and thus flooding may be just as severe with the storm center passing to the east as to the west.

Recent history—In the past 100 years, both the vegetational and physiographic aspects of Shackleford Banks have undergone radical changes, which of necessity must have altered profoundly the general facies of the vertebrate fauna. Detailed comparison between past and present, with reference to the vegetation and the shore lines, is made possible by the U. S. Coast and Geodetic Survey's topographic surveys, which form the base of their coast and harbor nautical charts. The oldest available surveys of Shackleford Banks were made in 1851 and 1853; the latest available to me is an advanced manuscript drawn from aerial photographs taken in 1946, and revised to November 30, 1949 on the basis of subsequent field inspection; thus, between them, they span nearly a full century (figs. 4-7).

Whereas the woodland now is confined to a relatively narrow strip between The Mullet Pond and Whale Creek Bay, in 1851-53 virtually the entire island, except the salt marshes, was heavily wooded. On the westward third of the island, the woods extended beyond The Mullet Pond towards Shackleford Point, and from the sound to the ocean. Eastward of Whale Creek Bay, where now is an unbroken grassland, devoid even of brush, the woodland extended all the way to the tidal flat westward of Cape Lookout. That this was a real woodland, and not merely a grassland interrupted by thickets, is evidenced by the conspicuous labelling of this area on the old charts as "Lookout Woods."

From these surveys, mapped on a scale either of 1:10,000 or 1:20,000, it is possible to calculate the areal extent of the woodland with a reasonable accuracy. In 1851-53, the wooded area occupied about 1250 acres, roughly 2 square miles; of this, in 1948, only 180 acres, or about 15 percent, remain. Eastward of Whale Creek Bay, in 1851-53, Lookout Woods covered about 400 acres; now, with the minor exceptions of Sam Winters Lump and Bells Island, neither of more than 1 acre, Lookout Woods has disappeared completely. Not a single living tree remains. In its place is a grassland, which is invading the salt marshes bordering the sound, as the level of these is raised by the blow-off of sand from the upper part of the ocean beach.

Between Shackleford Point and Whale Creek Bay the woodland covered about 850 acres in 1851-53; about 20 per cent of this remains as the present

woodland. The other 650-700 acres has been reduced to a barren waste-land of sand, absolutely lacking in vegetation.

These two parts of the island, to either side of Whale Creek Bay, evidently had quite different histories. From Whale Creek to The Mullet Pond the immediate cause of destruction of the forest, whatever the initiating factors, is clearly evident, since it is still at work. Here a wall of sand is advancing across the island, literally burying the woodland as it creeps along (fig. 8). Lewis (1917) estimated its progress at 4 to 12 feet per year. (At this rate, in another 50 to 100 years Shackleford Banks will be a real sand-strand, without a tree on it.) Occasionally, along the top of the sand wall, one sees what appears at first glance to be a clump of prostrate junipers; each such clump is really the crown of a red cedar 15 to 20 feet high—the rest of the tree is buried in the sand.

On the sandy wasteland between the sand wall and the ocean beach stand numerous skeletons of red cedars (fig. 10). The outermost of these trees, toward the ocean beach, must have been killed by salt-spray and by wind-driven sand. As the shifting sand moved inland, the wall was gradually built up, the prevailing on-shore (SW) winds picking up the loose surface sand and dropping it over the lee of any obstruction, where it comes to repose at an angle of approximately 30° . As the wall built up in height, it buried and smothered all vegetation; as it moved onward inland, the dead trees were again uncovered, and the bark and outer layers removed by the constant blast of wind-driven sand. Occasionally, one or more of these trees seem to have formed the nucleus of a dune.

Eastward of Whale Creek Bay there is no sand wall, nor is it likely that one ever developed here. Whatever the cause of the destruction of the woodland, all traces of it have been removed by successive hurricane floods. However, a grassland has been developed in its place, and is extending itself into the salt marshes bordering the sound. That this is of relatively recent occurrence is indicated by reference to Lewis (1917) who found here "a sandy waste, with little or no vegetation." There appears to have been very little grassland on the island in 1851-1853.

According to Lewis, "before the Civil War, cutting of timber, coupled with forest fires, the grazing of cattle and sheep, and the inroads of gales, had broken the protecting wall of vegetation and allowed the sand from the beach to blow in on the trees. Slowly at first, and then more and more rapidly, the sand was blown in on the vegetation, killing or covering the existent plants."

It is my opinion that "the inroads of gales" deserve a greater emphasis than the other factors mentioned. There is no evidence that extensive logging ever was practiced; the "cutting of timber" was limited to the immediate needs of the inhabitants. The latter were primarily fishermen; they lived on the soundward side of the island, not on the ocean beach. The clearings were very small, sufficient for a house and garden. In 1851 there were only two such westward of Whale Creek Bay, and the total number here never exceeded a half-dozen. It is unlikely that at that time, or for some time afterward, the

vidently
ond the
factors,
dvancing
fig. 8).
his rate,
d, with-
es what
lump is
tree is

h stand
e trees,
y wind-
ly built
ce sand
pose at
ied and
es were
nt blast
to have

How-
elf into
occur-
sandy
y little

ed with
es, had
e beach
lly, the
ants."

emphasis
logging
the needs
on the
s were
ly two
ceeded
rd, the

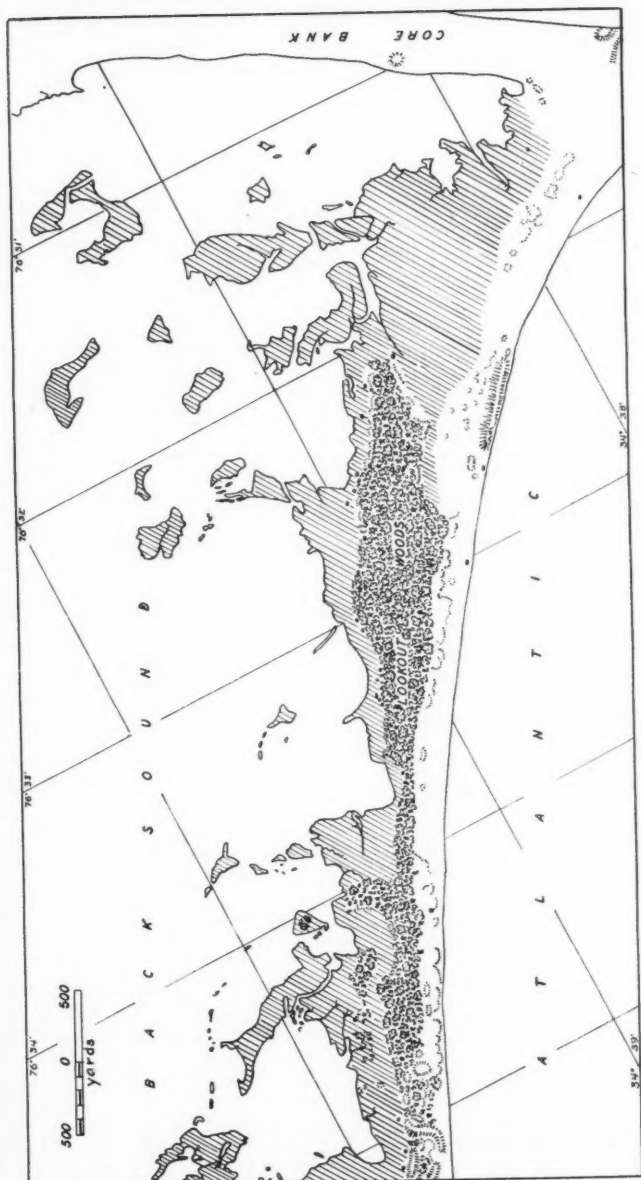


Fig. 6.—Eastern half of Shackleford Banks; topography and vegetation in 1853.
(Adapted from U.S.C. and G.S. topographic survey T-416.)

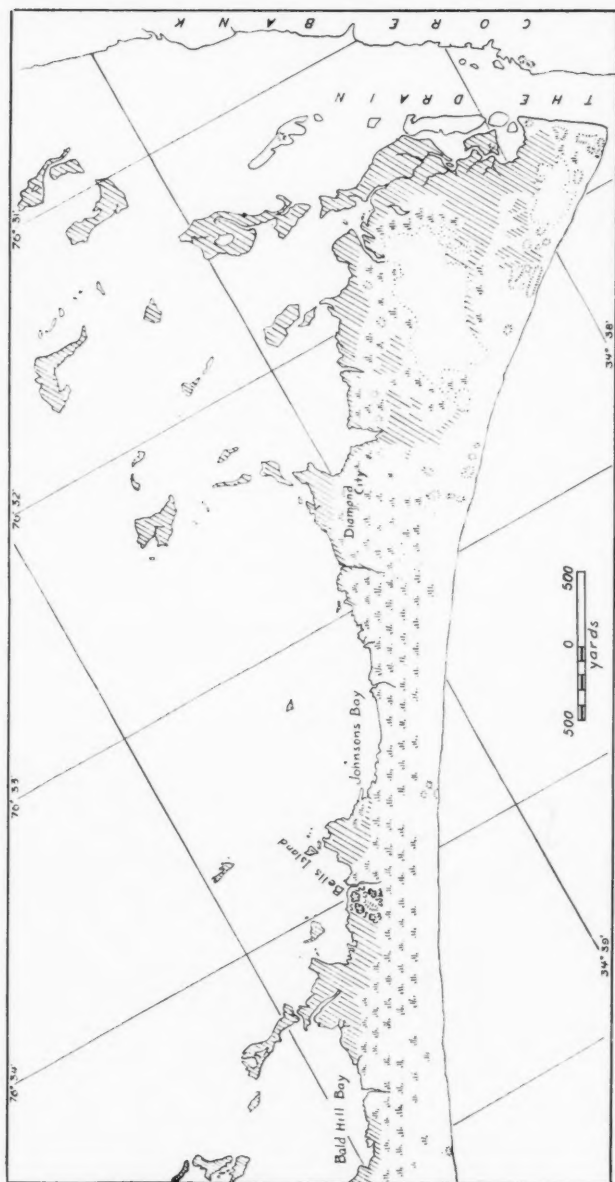




Fig. 8.—Upper: Looking out over the woodland, toward Back Sound, from the sand wall. In the foreground, sticking up out of the sand, the crown of a live oak; the rest of the tree has been buried. June 13, 1948. Lower: The sand wall advancing over the woodland; live oak and red cedar. June 13, 1948.

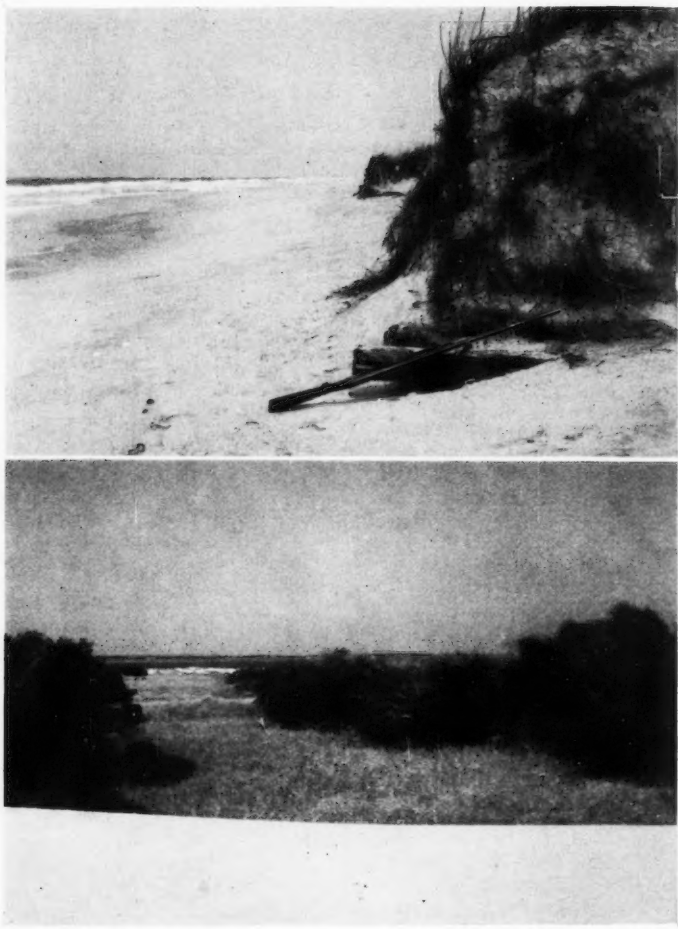


Fig. 9.—*Upper*: The sea has here eroded the outer beach to these outermost dunes, which are now being cut away. June 13, 1948. *Lower*: Just eastward of The Mullet Pond, the sand wall has reached a marsh extending into the live oak—yaupon thicket-woodland from the inner beach. In the marsh just below the sand wall *Rana pipiens*, *Gastrophryne* and *Hyla squirella* breed; mud turtle, Carolina wren, cardinal and red-wings found here also. March 17, 1950.

number of sheep on the island was great enough to seriously decrease plant reproduction.

On the other hand, there is abundant evidence that rooted trees and other vegetation on low ground cannot withstand the forces of hurricane floods. Welch (1885) quotes the testimony of Hatteras natives on the formation of the present Hatteras Inlet, between Hatteras and Ocracoke Island. The area was wooded, with yaupon holly and live oaks; there were a few homes in the neighborhood. Following the night of a hurricane's passage (Sept. 7-8, 1846), "In the morning they saw the sea and sound connected together, and the live oaks washing up by the roots and tumbling into the ocean." On the eastern end of Harker's Island, in the neighborhood of Shell Point, one today can see the stumps of numerous trees, including live oak and pine, barely emergent at low tide, still rooted in deep peat—evidence again that storm waters can wash away land covered by a vegetation of trees and grasses. Again, on the inner beach of Shackleford Banks, between High Hill Glade and The Mullet Pond one can see where recent storms have undercut the upper-beach ridge and washed out thickets of red cedar and yaupon holly.

Relative instability appears to be a prime characteristic of off-shore bars, especially these of the North Carolina coast, which are frequent hurricane targets. Just one hurricane and flood, sufficiently violent, could start the process of deterioration, even minor ones would then carry it along, aided meanwhile by the persistent, daily, strong, on-shore winds in moving the exposed sands inland. It is a matter of record that exceptionally severe storms occurred in 1933, in 1899, in 1885 and evidently also in 1846 (date of opening of Hatteras Inlet). It is perhaps significant that the general migration of the islanders to Harkers Island, which eventually left Shackleford Banks deserted, was begun and largely completed in the first decade of this century, thus following close upon the storm of 1899, and within 20-30 years of the "great" hurricane of 1885.

As to physiographic changes other than those directly related to vegetational changes, we have already noted the separation of Shackleford Banks from Core Banks and Cape Lookout through the formation of The Drain following the hurricane of September 16, 1933. But the most radical change in the configuration of the island has occurred at its westward extremity. Since 1851, it has been cut back not only from the seaward and soundward sides, but Beaufort Inlet has washed away a very considerable portion of the point. As measured along the $34^{\circ} 41'$ parallel, the point has been cut back about 650 yards, not including an outlying recurved spit. As measured along the $76^{\circ} 39'$ meridian, the seaward beach has been cut back about 380 yards, the inner (lagoon) beach about 155 yards, thus reducing the width here by nearly one-half (about 1160 yards to about 625 yards). Westward of The Mullet Pond about 180 acres has thus been washed away. Only the outer fringe of this was beach in 1851; the rest was not simply a tidal sand flat—there were about 50 acres of grassland back of an encircling area of dunes, and, on the soundward side, about 20 acres of woodland (fig. 4). All of this

has been washed away. Actually, the cutback of the point along the $34^{\circ} 31'$ parallel, since 1851, had amounted to almost 900 yards by 1946, but between 1946-49, the shore was again built out here about 225 yards!

There is evidence, also, that the bank is retreating northward, toward the mainland; comparison of the U. S. C. and G. S. topographic surveys of 1851-1853 and 1949 reveals that during this interval the ocean beach has moved northward from 40 to 150 yards along virtually its entire length. Only near The Drain, on the shore of Lookout Bight in the protection of Cape Lookout, has the beach been built out, apparently about 50 yards. As measured along the meridians from $76^{\circ} 38'$ eastward to $76^{\circ} 33'$, at $1'$ intervals, this northward retreat of the beach amounted approximately to 70 yards, 60, 40, 70, 140 and 155 yards. According to Johnson (1919) this is a normal process in the development and history of off-shore bars; the waves tear at the seaward face of the bar, on-shore winds pick up sand from the eroding outer beach and drop it on the bar, gradually building up the inner beach on the lagoon. By this combination of processes, the bar creeps slowly landward, until it comes to rest against the shore.

On Shackleford Banks the cutting back of the ocean beach is evidently a continuing process, as would be expected. According to measurements furnished me by the U. S. Coast and Geodetic Survey, and taken by them at my request from their original surveys, the outer beach retreated northward along its entire length in the short interval of 1933-1949. Near $76^{\circ} 36'$ this amounted to about 30 yards, near $76^{\circ} 38'$ to about 80 yards.

However, the inner beach has nowhere kept pace, in its growth, with the retreat of the outer beach, and, indeed, fails to conform to the Johnsonian theory. Westward of High Hill Glade, a very considerable amount of the inner beach has been cut away (fig. 4). On this section of the island, apparently, the wind-borne sand of the eroding ocean beach is piling up on the woodland; little, if any, of it is reaching the island's inner beach. The latter is exposed to the action of storm tides, which here run parallel to its shore. Such floods as that of September 1933, being unable to escape across the island because of its higher elevation westward of Whale Creek Bay, rush toward Beaufort Inlet along the inner beach, gouging out its shoreline.

But recently, at least, there has been some out-building of the inner beach between High Hill Glade and Whale Creek Bay. This amounted to about 15 yards in the period 1933-1949.

Eastward of Whale Creek Bay, the inner shoreline as a whole does not appear to have moved appreciably northward, despite the cutting back of the ocean beach. However, several small bays and coves have been filled up, smoothing out the shoreline particularly of Bald Hill Bay and Johnsons Bay. Much of the wind-borne sand appears to have gone into raising the level of the salt marshes, with the consequent replacement of marsh by grassland. In a few places this process has extended to the shore of the sound, with the marsh replaced by a sandy beach. In 1853, the sound was continuously bordered by salt marsh eastward of Whale Creek Bay, but there are now

(1949) sand beaches about 300 yards long on Bald Hill Bay and at Bells Island, and one about 1200 yards long on Johnson's Bay (figs. 6, 7).

On the U. S. C. and G. S. topographic survey of 1853 there may be seen about 20 dwellings along the soundward margin of Lookout Woods. This area eventually came to be called Diamond City; most of the islanders lived in this neighborhood, although there were some dwellings all along the soundward shore of the Banks. At the turn of the century, Diamond City was evidently a place of some importance in this section of coastal North Carolina. R. E. Coker, who was director of the U. S. Fishery Biological Laboratory at Beaufort 1902-1904 recalls a movement at that time to extend the railroad across the sound to the Banks, to develop Diamond City as a port, though nothing came of this. Shortly thereafter a general exodus of the islanders took place, most or all of them eventually moving to Harkers Island. Nothing remains now but an occasional loose pile of bricks or stone, marking the foundations of a former dwelling place, and several large mounds of oyster shells, now covered by sand. The hurricane flood of 1933 washed out the cemetery; we found only a single stone in 1940 (fig. 13).

Semi-feral domestic animals.—Horses, cattle, sheep, goats, pigs and housecats live on the island in a semi-wild state. The horses have been famed since colonial times as the "bank-ponies"; they are popularly supposed to have reached the outer banks through the wreck of an early colonial Spanish vessel. The ponies do not enter the woodland, but roam the grassland eastward of Whale Creek Bay, and frequently visit the numerous marshy islands. The goats seek shelter and forage in the outer margin of the woods next the sand wall, sometimes wandering about on the sandy waste of the dead forest. Sheep, cattle, and pigs move about the entire island except on the sandy waste; the pigs commonly forage on trash on the beach of Back Sound, and root in the grassy swales extending into the woodland from the upper beach. Eastward of Whale Creek Bay, sheep trails commonly transected the *Juncus* marshes and clumps of marsh-elder (*Iva*). They are by far the most numerous of the domestic animals on the island, and probably the most important of these in their effect on the habitat and natural fauna. I was unable to form a satisfactory estimate as to their numbers.

THE VERTEBRATE FAUNA

At least 34, and probably not more than 40, species of land vertebrates—amphibians, reptiles, breeding land birds, and mammals—occur on Shackleford Banks, as against about 186 species on the adjacent mainland (table 1). The island's fauna is thus reduced to about 20 percent of the fauna of the mainland. The amphibians show the greatest impoverishment (to about 15 percent), mammals and reptiles least (to about 25 percent). If there were 3 more species of amphibians on the island, their representation would be raised to 25 percent of the mainland fauna, but it is extremely unlikely that we overlooked as many as 3 species. On the other hand, it is entirely possible that as many as one-third of the mainland reptiles occur on the island (1 or 2

additional turtles, 2 or more additional snakes). Reptiles seem, in the aggregate, better suited to insular life, or at least to the essentially dry habitat conditions which prevail on such an island as Shackleford Banks.

It would be highly desirable, in a study of this sort, to compare the number of species on the island with the number of species occurring on the mainland in *habitats comparable* to those available on the island, rather than to the mainland population as a whole. However, the precise ecological require-

TABLE I.—Numerical comparison of tetrapod vertebrate fauna of Shackleford Banks with that of the immediate adjacent mainland

Taxonomic Group	Mainland	Shackleford Banks
Amphibia		
Caudata	11	0
Scaphiopodidae	1	1
Bufo	3	1
Hylidae	10	1
Ranidae	6	1
Brevicipitidae	1	1
Reptilia		
Crocodylidae	1	0
Sauria	8	4
Serpentes	29	6
Testudinata	10	2
Aves		
Falconiformes	6	0(= 1?)
Galliformes	1	0
Columbiformes	1	1
Cuculiformes	1	1
Strigiformes	4	0
Caprimulgiformes	2	1
Micropodiformes	2	0
Coraciiformes	1	0
Piciformes	7	0
Passeriformes	52	9(= 12?)
Mammalia		
Marsupialia	1	1
Insectivora	3	1
Chiroptera	4	0
Carnivora	8	0(= 1?)
Rodentia	10	2
Lagomorpha	2	1(= 2?)
Artiodactyla	1	0
Summary		
Amphibia	32	5
Reptilia	48	12
Aves	77	12(= 16?)
Mammalia	29	5(= 7?)
Total	186	34(= 40?)

ments, including minimum area of habitat, are not sufficiently known in altogether too many cases to make such a comparison feasible. In attempting to do so for one group, I was able to cut down the number of mainland birds from 77 to 54, with some degree of confidence. This would raise the percentage of mainland species of birds occurring on the island from about 20 to about 30 percent—still a considerable depauperation. Hatt *et al.* (1948), also, failed to find many species of birds on some Lake Michigan islands even though apparently suitable habitat conditions occurred; this in spite of the fact on occasion they did find individuals which by modifications of habit were able to occupy islands that were apparently unsuitable in the normal ecology of the species.

The terminology in the following lists, as in Table I, follows Stejneger and Barbour (1943) for amphibians and reptiles, the American Ornithologists' Union (1931) for birds, and Miller (1924) for mammals.

AMPHIBIA

Present: *Scaphiopus holbrookii*—Spadefoot; *Bufo w. fowleri*—Fowler's toad, "toad-frog"; *Hyla squirella*—Tree frog; *Rana p. sphenoccephala*—Leopard-frog; *Gastrophryne carolinensis*—Narrow-mouthed toad.

Probably absent: All urodeles? *Bufo quercicus*; *Rana clamitans*; *Rana catesbeiana*.

The toad (*Bufo w. fowleri*) is the most conspicuous amphibian, ranging over all of the island except the sandy waste. On June 11, 1948 (a bright, warm day) in a 2½ hour walk over the grassland between Whale Creek Bay and Bells Island, I counted 34 toads, most of them in the lower, more damp areas, but 7 in the very dry, inner dune-edge zone (figs. 10 lower, 12 lower, and 13). They are also abundant in the woodland—one evening 12 were to be seen at one time in the very small clearing around camp. They were seen occasionally also on the beach at Wade Shore; one evening one was collected at the every edge of the beach, and entered the salt water in attempting to escape. On May 6, 1950, an adult male was collected on the small island, lying off from Bells "Island" (fig. 7), known as Cows Island. The latter is slightly elevated in its center, with a relatively heavy vegetational cover, including wax myrtle and yucca. A Cows Island breeding population is a virtual impossibility, since the only depression is a large shallow area, separated from the sound by a very low beach ridge, and containing water very salty to the taste. At its nearest point, Cows Island is 140 yards from the shore of Shackleford Banks, and there is here a shoal, connecting the two, which is very likely uncovered at extreme low water, although it was not uncovered by the low tide at the time of our visit. This shoal most probably provided the route of invasion of Cows Island; the observation indicates that Fowler's toad at least occasionally wanders about on exposed tidal flats and in the intertidal zone.

On this same day, literally scores of small toads were encountered on the grassland between Bells Island and the ocean beach. About 30 were carefully scrutinized to check against the possibility of being *B. quercicus*, but all proved to be young Fowler's toads. The snout-vent length of 9 which were collected

ranged from 31 mm. to 39 mm. (aver., 33.4 mm.). Although it was mid-day, the sky cloudless, and the sun very hot, almost all of these little toads were found on sandy areas with a very scant vegetation, not in the thick grass. It has been our general experience that adult Fowler's toads also are not confined to wet or damp areas, or to nocturnal activity—they were encountered frequently on the bare dune-sand of clearings in the woods, even on bright days when this sand was distinctly hot.

In the thicket-woodland, where it is very common, *Hyla squirella* is to be heard at all hours, even occasionally in the middle of a hot, bright day. It apparently is not confined to the latter habitat, since on May 11, 1940, two were found at Sam Winters Lump, one in a log, the other on a log which was surrounded by several yards of bare, dry sand. Again, on May 6, 1950, 4 males and a female, squatting side by side, were uncovered in a large piece of shipwreck timber lying out in the grassland about 250 yards from Bells "Island." The latter consists of a few low sand dunes, without a surface cover, but bearing a single almost prostrate live-oak with very little foliage, and about a dozen small (10-15 ft.) toothache trees (or southern prickly ash, *Xanthoxylum clava-herculis*); there is not another single tree or bush for many miles to the eastward, or for 2500 yards to the westward (Sam Winters Lump). In addition to these specimens from far out on the grassland, a pair were found in a rotted live oak log on the dune margin of Bells Island.

The southern leopard frog (*Rana p. sphenoccephala*) is less abundant than the *Bufo* or *Hyla*, but numbers of small individuals were seen, and a few collected, about the margins of small pools, chiefly just back of the inner beach and along the margins of the thicket woodland. None was found around the pools of the grassland.

Gastrophryne carolinensis is not uncommon, but it is very inconspicuous. Only two ever were seen in the open, both on a damp, dark afternoon following a rain. Many were found within well-rotted but relatively dry pine logs, or beneath logs, or buried at the base of small fallen trees, within the disintegrating butt.

The oak-toad (*Bufo quercicus*) is quite common on Harkers Island, barely more than 2 miles away, between Shackleford Banks and the mainland, occurring there in sandy woodland, but also along the marsh edge, and found occasionally on the beach. Essentially similar habitats occur extensively on Shackleford Banks, but we never have found the oak-toad there.

In 28 nights on the island in 1939, 1940, and 1948, and many more days, I have never heard either *Rana clamitans* or *R. catesbeiana*.

It is quite unlikely that any urodeles occur on Shackleford Banks, but one cannot speak of their absence with assurance, because of the secretive habits of this group. On Harkers Island, I found the newt (*Triturus*) on my first visit there, in 1939; but I found no other salamanders until 1949, when we turned up, on the same day, a young slimy salamander (*Plethodon glutinosus*) and an as yet unidentified larva (not *Triturus*). Coues and Yarrow (1878) list the "red-backed salamander" ("*Plethodon cinereus erythronotus*") as

"common" in this vicinity, but so far as anyone has been able to discover since, *P. cinereus* does not occur in North Carolina below the piedmont, and there only in cold pockets on steep, north-facing slopes, along with some elements of the North Carolina mountain flora.

REPTILIA

Present: *Anolis carolinensis*—Chameleon; *Ophisaurus ventralis*—Glass-snake; *Cnemidophorus sexlineatus*—Swift, "sand lizard," "striped lizard"; *Eumeces inexpectatus*—Coastal Plain blue-tailed skink; *Rhadinæa flavilata*—Yellow-lipped snake; *Opheodrys aestivus*—Rough green-snake; *Coluber constrictor*—Black-snake, "Horse racer"; *Elophe quadrivittata*—Chicken-snake; *Natrix sipedon*—Water-snake; *Thamnophis* [*sauritus*?—Ribbon-snake]; *Kinosternon subrubrum*—Mud-turtle, "Hickity"; *Malaclemys centrata*—Diamond-back terrapin.

Probably absent: Alligator; *Crotalid* snakes (except *Sistrurus miliarius*?); *Eumeces fasciatus*.

The swifts or "sand lizards" (*Cnemidophorus sexlineatus*) are exceedingly common on the island, and are probably the most abundant of all vertebrate species, as well as the most wide-spread ecologically. They were to be seen, during the day, at almost any moment in the thickets and woods about camp (fig. 10 lower); they were found conspicuously on the sand dunes, where sea-oats (*Uniola*) form the only cover and among the roots of which they usually skittered, sometimes taking refuge in the burrow of a ghost-crab; and they were very common on the grassy sand flats east of Whale Creek Bay (fig. 13). All of these were "dry" situations, however; no swifts were seen in damp or marshy ground, although, on the flats, they were seen right up to the dry, sandy edge of shallow pools and marshes, within a few inches of the water.

Also abundant, but decidedly inconspicuous, are the blue-tailed skinks (*Eumeces inexpectatus*). On the morning of May 11, 1940, a group of 8 students found more than 20 skinks, exposing them literally everywhere that fallen logs or dead standing trees with loose bark occurred, within and under the logs, and beneath loose bark.

The so-called "chameleon" (*Anolis carolinensis*) is fairly common, occurring both in the low woods (fig. 12 upper) and in the red cedars on top of the old dunes (fig. 10 lower). The remaining lizard, the "glass-snake" (*Ophisaurus ventralis*), is most inconspicuous, because of its habits. Only two were seen on Shackleford Banks, both in July, 1940. One was collected from the water at the edge of The Mullet Pond, and one encountered in yaupon thickets on the side of the old dune known as High Hill.

Only *Natrix*, among the snakes, is frequently seen. These banded water-snakes are relatively abundant in The Mullet Pond, and may be found in almost any of the small pools that occur on the island. None of the other snakes was encountered in numbers. *Thamnophis* was seen only once; in 1939 I came upon one draped across the top of a low shrub at the edge of a marsh west of High Hill glade. It made off rapidly into the tall grass of the marsh on my approach. From the brief glimpse, I judged it to be a ribbon-snake, *T. sauritus*, rather than the common garter-snake, *T. sirtalis*, an opinion the

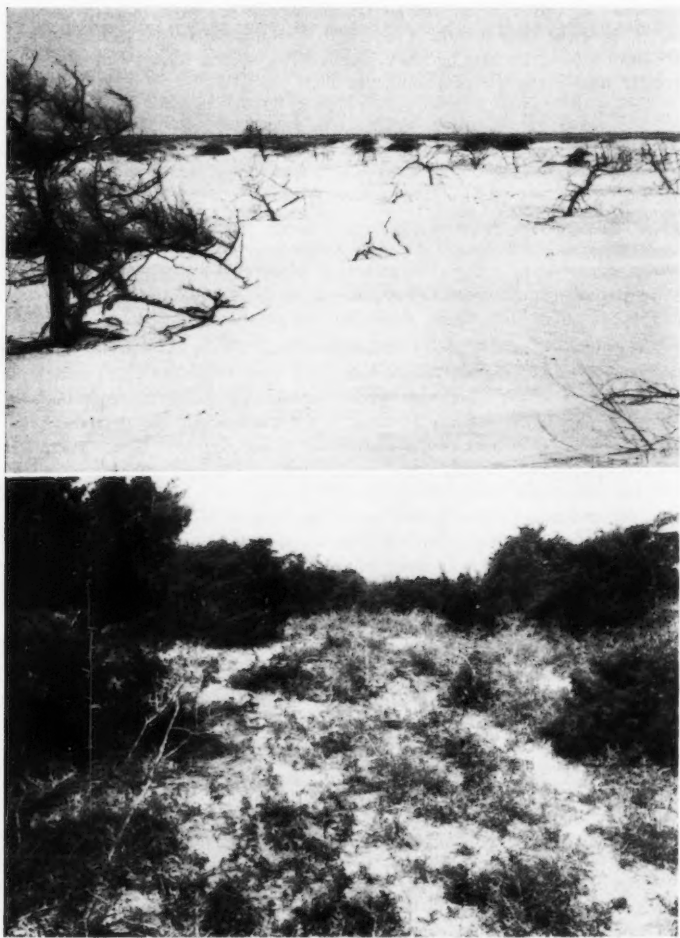


Fig. 10.—*Upper*: The dead *Juniperus* woods, nesting area of crested flycatchers. Small dunes in background covered with sea-oats: a few house-mice occur here. March 17, 1950. *Lower*: an opening in the dry thicket-woodland; low forms of yaupon holly in the foreground, red cedar to the left, loblolly pine, live oak and red cedar in the background. Habitat of painted bunting, cardinal, Carolina wren, swift or sand lizard, Carolina chameleon, and Fowler's toad. June 13, 1948.

habitat would tend to confirm. Only one chicken-snake (*Elaphe quadrivittata*) was seen; this was collected (May 11, 1940, Sam Winter's Lump) from beneath loose bark of a live-oak, about 10 feet above the ground. But the shed skin of a young specimen, 15 inches in length, was taken later on the same day from a large tree-trunk, 5 feet up, in the woods about 2 miles distant. This skin has been lost, unfortunately, so it is not now possible to say with certainty whether it was a young gray rat-snake (*E. obsoleta confinis*) or a young *E. quadrivittata*. On July 22, 1940, again at Sam Winters Lump, the freshly shed skin of a chicken-snake was found 8 feet up on one of the old live oaks.

Two yellow-lipped snakes (*Rhadinaea flavilata*) were taken in 1939; one was found under the debris of sticks and strips of bark beneath a dead, standing pine tree, and another was uncovered while stripping loose bark from a pine log. These specimens (and some collected by me on Harkers Island) extend the known range of this species some 15 to 20 miles to the northeastward, since the extreme in this direction previously was the first known individual of the species, collected by H. C. Yarrow in 1870, the type locality being 8 miles south of Fort Macon, on Bogue Banks. According to Brimley (1942) the only North Carolina record of *Rhadinaea flavilata* other than the type specimen "is of one taken by Dr. Karl P. Schmidt on July 9, 1915, under a pine log near Councils, in Bladen County."

The rough green-snake (*Opheodrys aestivus*) is more commonly met with, on all of the islands, perhaps because its habits make it relatively more conspicuous than other snakes. On Shackleford Banks we saw three one morning, in 1941, at Sam Winters Lump, two of which were high in the live-oaks and one on a low-lying pepper vine growing over a sandy hump. In June, 1948, I collected one as it was lying in the sun on top of a tall bunch of grass in a sandy glade within the woodland.

The black-snake (*Coluber constrictor*) was quite uncommon, in my experience, as I found only two; but Mr. Starling Lewis, of Harkers Island, who as a boy lived on Shackleford Banks, said he remembered it as the commonest snake on the island.

The two turtles (*Kinosternon* and *Malaclemys*) while not uncommon, seemed to me to be decidedly less numerous than I had found them on Ocracoke Island (Engels, 1942).

The alligator has been recorded in all of the coastal counties of North Carolina south of Albemarle Sound, occurring in all of the rivers coming down to the coast in this region. But although at least one once reached Shackleford Banks, to be killed by fishermen in The Mullet Pond, the species cannot be reckoned as a permanent member of this island's fauna.

Five crotalid snakes, all very poisonous, occur in the North Carolina coastal plain. These are the canebrake and diamond-back rattlesnakes (*Crotalus horridus* and *C. adamanteus*), the pygmy or ground rattler (*Sistrurus miliarius*), and the copperhead and cotton-mouth moccasins (*Agkistrodon mokeson* and *A. piscivorus*).

The evidence against the presence of any of these on Shackleford Banks,

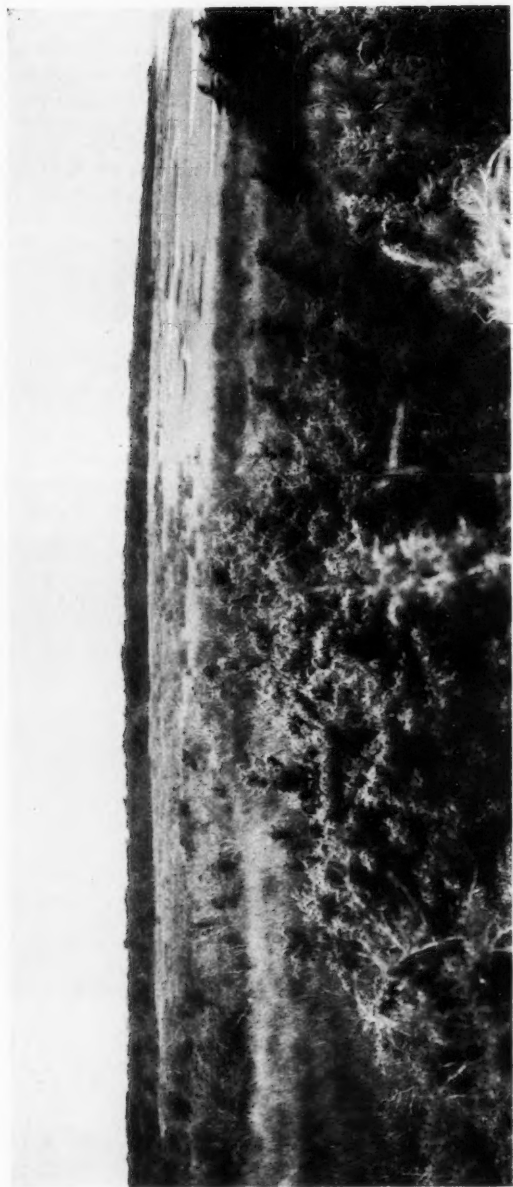


Fig. 11.—High Hill Glade and thicket-woodland, looking westward from High Hill; Back Sound to the right. Here rice rats, banded water-snakes; on the margins, house mice, Carolina wrens, and red-wings. June 13, 1948.

except for *Sistrurus*, is all indirect, based on the experience of the Harkers Islanders. Many of these men were born on Shackleford Banks and lived there as boys, most of them have spent considerable time on the island in recent years, and most of them have some knowledge of these poisonous snakes. They know the copperhead, which occurs on Harkers Island, but they are agreed there are none on Shackleford Banks, nor had anyone ever heard of a rattlesnake or cotton-mouth moccasin there. Coues and Yarrow (1878) writing of *Sistrurus miliarius* [*Caudisona miliaria*] said: "... quite common on Shackleford Banks. . . . It is a fact worthy of remark, that, while on Bogue Banks, rattlesnakes and moccasins are extremely abundant, this is the only venomous species found on the neighboring island of Shackleford." When I told Mr. Starling Lewis, one of the Harkers Islanders born on Shackleford, that an Army doctor, writing at Fort Macon 70 years ago, had said there was a species of rattlesnake on Shackleford, his reply was: "Maybe he meant what we call a 'ground rattler,' a little brown snake about 10 inches long—but he isn't a real rattlesnake." I failed to find any *Sistrurus* on Shackleford, but that of course is not proof that they have disappeared in the 80 years since Coues was there.

Dr. J. Bailey, of Duke University, an experienced herpetologist, has told me he saw (but did not capture) a cotton-mouth moccasin in The Mullet Pond, in the spring of 1948. In 1938, Mr. John Russell, of Harker's Island, from his boat shot a large rattlesnake as it was swimming in Beaufort Inlet, near the Shackleford Point breakwater. I was told of another being killed off Harkers Island, in Back Sound. Coues and Yarrow (1878) also noted reports of rattlesnakes and cotton-mouths seen swimming in the Sounds. It is quite possible that Dr. Bailey's cotton-mouth represents a recent invasion of Shackleford by an individual snake.

Although both *Eumeces fasciatus* and *E. laticeps* occur in the North Carolina coastal plain, apparently neither has reached Shackleford Banks; every blue-tailed skink collected there is clearly referable to *E. inexpectatus* Taylor (Engels, 1949).

AVES⁴

Present: *Cathartes aura*—Turkey vulture (Probably casual only); **Zenaidura macroura*—Mourning dove; *Coccyzus (americanus?)*—Cuckoo, "rain-crow"; *Aniostomus carolinensis*—Chuck-wills-widow, (Irregularly?); **Myiarchus crinitus*—Crested flycatcher, "French mocker"; *Progne subis*—Purple martin; *Corvus ossifragus*—Fish crow; *Penthestes carolinensis*—Carolina chickadee (Irregularly?); †*Thryothorus ludovicianus*—Carolina wren; *Vireo griseus*—White-eyed vireo (Irregularly?); *Vireo olivaceus*—Red-eyed vireo (Irregularly?); *Dendroica discolor*—Prairie warbler (Migrant only?); †*Sturnella magna*—Meadowlark, "field-lark"; †*Agelaius phoeniceus*—Red-wing, "jack," "jackdaw"; **Casidix mexicanus*—Boat-tailed grackle, "blackbird"; †*Richmondia cardinalis*—Cardinal, "red-bird"; †*Passerina ciris*—Painted bunting.

* Nests.

† Other evidences of breeding observed, such as fledglings, brood-patch of females, enlarged testes of males.

⁴ Only those land birds occurring in the breeding season, i.e., exclusive of all waders, shore and aquatic birds, migrants and winter visitors.

Probably absent: *Chaetura pelagica*—Chimney swift; *Picidae*—Woodpeckers; *Hirundo rustica*—Barn swallow; *Sitta carolinensis*—White-breasted nuthatch; *Sitta pusilla*—Brown-headed nuthatch; *Telmatoodytes palustris*—Long-billed marsh wren; *Mimus polyglottos*—Mockingbird; *Geothlypis trichas*—Maryland yellow-throat; *Pipilo erythrophthalmus*—Towhee; *Ammospiza maritima*—Seaside sparrow; *Melospiza melodia*—Song sparrow.

The avifauna of Shackleford Banks is even less varied than this meager list would indicate. Four of the seventeen species were observed each only once: Cuckoo (*Coccyzus*), June 10, 1948; chickadee (*Penthestes carolinensis*), July 21, 1940; white-eyed vireo (*Vireo griseus*), July 21, 1940; and red-eyed vireo (*V. olivaceus*), June 25, 1939. The latter three are frequently met on Harkers Island; our experiences would suggest that just an occasional individual or two sometimes wanders to Shackleford, and that these species should not be reckoned in the breeding population.

In June, 1948 there were at least four singing chuck-will's-widows (*Antrostomus carolinensis*) in the woods, between The Mullet Pond and Whale Creek Bay, but probably not any more. This bird was not heard either in 1939 or 1940. I suspect that the relatively small area and its relative isolation accounts for this fluctuation in numbers especially with a bird such as this, which anywhere must be less numerous than the smaller song-birds.

The turkey vulture (*Cathartes aura*), almost certainly, and perhaps also the purple martin (*Progne subis*) are casuals, the former as a wide-ranging forager, the latter as a wanderer in the pre- and post-breeding season. Fish crows (*Corvus ossifragus*) are regularly seen foraging on both the inner and outer beaches, but no nests were found. The woodland is not extensive, and the neighboring mainland, at its nearest point less than two miles distant, with marshy islands and shoals intervening, is probably well within the normal foraging range of these birds. It is entirely likely, then, that fish crows use Shackleford Banks only as a feeding ground. The prairie warbler (*Dendroica discolor*) was seen and heard in numbers on one-day visits in May (1940, 1941, 1946) but not recorded once during the extended visits of June and July (1939, 1940, 1948). Therefore, although it is certainly a breeding bird on nearby Harkers Island, it appears to be solely a migrant on Shackleford Banks.

The eight remaining species occur in considerable numbers and all most probably breed on the island, although direct evidence is lacking for some. These breeding birds form two distinct ecological groups, four of the species being primarily grassland birds, four belonging to the thicket-woodland. The meadowlark (*Sturnella magna*) is restricted to the grassland, eastward of Whale Creek Bay. The mourning dove (*Zenaidura macroura*) is also fairly abundant there—the only nest observed was on the ground, well concealed by the knee-high *Spartina* grass; but it also was usually seen over the waste-land of the dead forest, and in the dunes area. The red-wings (*Agelaius phoeniceus*) were very conspicuous on all the marshes, including the small ones that indent the woodland. The habitat requirements of the boat-tailed grackles (*Cassidix mexicanus*) are somewhat different—they forage solely on the marshes or open grassland, but nest and roost in trees or tall thickets. Hence

rs; *Hirun-*
pusilla-
mus poly-
Maryland
sparrow;

meager
ch only
ensis),
red-eyed
tly met
nal indi-
should

(*Antro-*
Whale
ither in
solation
as this,

ps also
ranging
Fish
er and
ve, and
distant,
normal
ws use
ndroica
(1940,
and July
bird on
Banks.
l most
some.
species

The
ard of
fairly
led by
e-land
phoeni-
s that
ackles
n the
Hence



Fig. 12.—Upper: Lowland woods. *Hyla squirella* and Carolina chameleon are common here. June 28, 1939. Lower: Sam Winters Lump, an isolated remnant of the woodland (see figs. 4, 5); nesting site of boat-tailed grackles. Also found here: *Hyla squirella*, blue-tailed skink, "sand" lizard, rough green-snake, *Elaphe q. parallela* (type locality); Fowler's toad and sand lizards common on the grassy flat in foreground. Spike-rush marsh to the left. June 25, 1939.

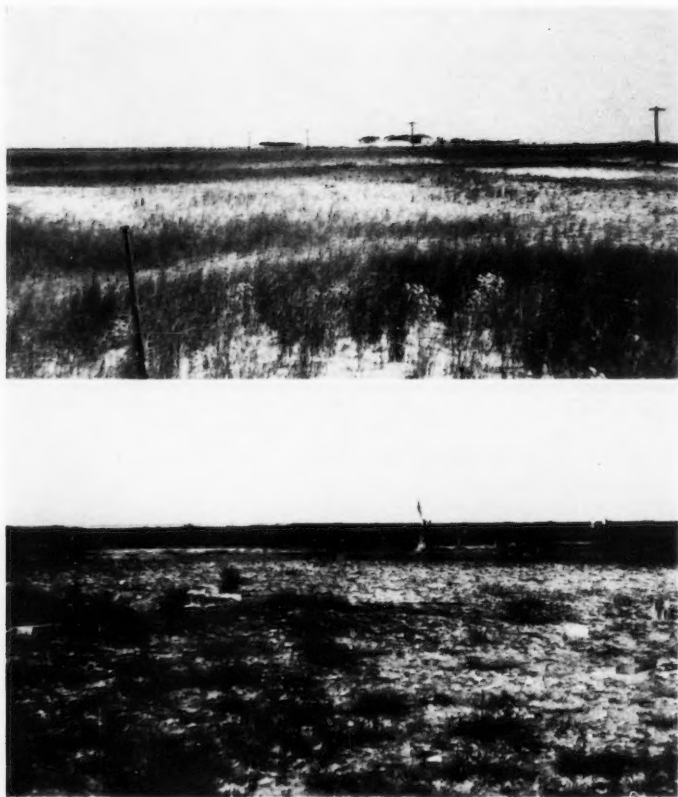


Fig. 13.—*Upper*: Sandy and grassy flat typical of eastern half of island; common here: Fowler's toad, "sand" lizard, meadow-lark, mourning dove, red-wing; a few house mice; foraging area for boat-tailed grackle; *Hyla squirella*, at least occasionally. Bells "Island," the only existing remains of Lookout Woods, in background. (See figs. 6, 7.) June 21, 1939. *Lower*: Remains of a cemetery on site of Diamond City, the broken tree-trunk (center) the only reminder of the once extensive woodland. May 19, 1940.

I have found them only on Sam Winters Lump and Bells Island (figs. 12 lower, 13 upper)—small "islands" of trees between marsh and grassland. They do not occur on the margins of the thicket woodland where there are small marshes, as do the red-wings.

Just four species make up the bulk of the bird population within the thicket woodland—Carolina wren (*Thyothorus ludovicianus*), cardinal (*Richmondia cardinalis*), painted bunting (*Passerina ciris*) and crested flycatcher (*Myiarchus crinitus*). The latter was found nesting in the dead forest (fig. 10 upper) in 1939 and again in 1948, but foraged almost exclusively in the woodland (Engels, 1949); the other three are entirely restricted to the thicket-woodland. All of these are numerous and can be heard in any part of the woodland almost any time. Four of five adult singing male buntings collected in June, 1948, had not yet acquired the "painted" plumage. Nothing seems to have been published concerning the age at which this "adult" plumage is attained, or of variation in this respect, individual or geographic.

The song sparrow (*Melospiza melodia*) is abundant on Ocracoke Island, but near there reaches its southern-most coastal distribution. This was previously noted (Engels, 1942) as being evidence of an "intangible barrier" which delimits a species' range. But perhaps it should be pointed out that below Ocracoke there is a gap of 30 to 40 miles in habitat suitable to song sparrows. From Whale Creek Bay on Shackleford Banks northeastward nearly the whole length of Core Banks the vegetational cover consists solely of grass without thickets or shrubs, hence without song sparrow nesting sites. This may be an important factor in limiting a southwestward extension of range of the song sparrow along these coastal islands.

Burleigh (1937) thought he was able to demonstrate, in the Beaufort area, a gap in the range of marsh wrens between *Telmatodytes p. waynei* to the north and *T. p. griseus* to the south. However, T. L. Quay (personal communication) reports this marsh wren to have unusually narrow and rigid habitat requirements, not generally met with in the Beaufort region; but where the habitat occurs he finds them to be quite abundant, as on certain marshes along the North River, apparently overlooked by Burleigh. Their absence from Shackleford Banks, then, may be ascribed to a habitat deficiency.

The absence of seaside sparrows (*Ammospiza maritima*) however, cannot be ascribed to lack of suitable habitat. There are extensive areas of spike-rush (*Juncus*) such as are occupied by these sparrows on Ocracoke Island (Engels, 1942) and on nearby Harkers Island, but thorough and repeated searches failed to turn up any sparrows. The spike-rush marshes, however, are criss-crossed by trails of the many semi-feral domestic animals of the island; and it is quite likely that these animals, particularly the many hundreds of sheep, by their disturbance have driven out the ground-dwelling seaside sparrows.

The almost complete absence of buildings on the island undoubtedly is sufficient to account for the absence of chimney swifts (*Chaetura pelagica*), barn swallows (*Hirundo rustica*) and English sparrows (*Passer domesticus*).

But I am unable to account for the virtually certain absence of yellow-throats, towhees and the three mimids.

MAMMALIA

Present: *Didelphis virginiana*—Opossum; *Scalopus* sp.—Mole, "ground-mole"; *Oryzomys palustris*—Rice-rat, "marsh-rat"?; *Mus musculus*—House-mouse; *Sylvilagus palustris*—Marsh-rabbit.

Probably absent: *Chiroptera*—Bats; *Carnivora*—(except mink?); *Sciuridae*—Squirrels and chipmunks; Muskrats and other *Cricetidae* (native rats and mice) except *Oryzomys*; Deer.

The mammalian fauna of Shackleford Banks is decidedly poor, both in numbers of species and in numbers of individuals. Trapping was carried on only in 1939 (late June). In 532 "trap-nights" using from 30 to 70 oversized snap-back mouse traps, of the type known as "museum-special," the total catch consisted of 5 house-mice (*Mus musculus*) and 1 rice-rat (*Oryzomys palustris*). Of these 532 "trap-nights," 100 were in some open woods, relatively free of undergrowth, and with a grassy ground-cover; 102 were in more brushy woodland, composed chiefly of yaupon holly and red cedar, the ground cover being a litter of twigs and leaves; 30 were in a grassy swale extending into the brush; and 30 were along the margin of Sam Winters Lump, at the edge of the spike-rush marsh. None of these 262 traps captured anything at all, although the habitats appeared to be favorable to such small mammals as *Blarina* and *Peromyscus*. In the sea-oats covering some outer dunes (fig. 10 upper), 64 "trap-nights" resulted in the capture of 2 house-mice; two more were taken in 138 "trap-nights" on the grassy flat back of Whale Creek Bay (fig. 13 upper), a habitat in which one might reasonably have expected also *Reithrodontomys*, *Sigmodon*, and possibly *Microtus*, and another house-mouse and a rice rat were taken in 68 "trap-nights" along the margins of High Hill glade (fig. 11). A few rat-sized snap-back traps were set out at various times, for a total of 82 "trap-nights." Only 2 young opossums (*Didelphis virginiana*) were caught in these.

For the house-mouse, these figures are in sharp contrast to those obtained for similar habitats at the same time of year on Ocracoke Island (23 in 150 traps, June 16-17, 1941; Engels, 1942) and on Bogue Banks (7 in 24 traps, July 19, 1939). Evidence for a low population of rice-rats, however, is inclusive, since no winter trapping was done, and experience on Bogue Banks indicates that rice-rats cannot be taken in summer, not at least by ordinary trapping methods.

There are many feral domestic cats on the island, but, in my opinion, hardly enough for them to account for the low number of mice. The cats seem to feed largely on trash thrown up on the inner beach or trash dumped there by fishermen hauling along-shore for shrimp. There are many cats on Ocracoke Island also, where house-mice are abundant; but I have no data on relative abundance of cats on the two islands. On the other hand, there is one striking difference in the general aspect of the habitat which, conceivably, might be a factor—on Ocracoke Island, as also on Bogue Banks, house-mice

were most abundant in the sea-oats, and this covering is there everywhere interspersed with thickets ("dune-thickets," Engels, 1942, p. 297; fig. p. 282); the latter are entirely lacking on Shackleford Banks. These thickets may be essential to relatively high population numbers of mice, in providing nesting sites and cover. Also, according to Lewis (1917) the sea-oats "appear to set seed rarely in this locality." Certainly in late June 1940 this grass was conspicuously less luxuriant on Shackleford Banks than it was 3 weeks later on Bogue Banks; thus a lesser food supply may also be a factor limiting the mouse population on Shackleford Banks.

Moles are relatively abundant, judging from the numerous runways, which are to be seen in all parts of the woodland, on the grassy flats back of the dunes eastward of Whale Creek Bay, and occasionally even on the beach of Back Sound, down to the waters' edge. Very unfortunately I was unsuccessful in all attempts to secure specimens. The runways were undoubtedly those of the species *aquaticus*, but one might expect the individuals to show signs, in their variation, of some differentiation due to their isolation.

Only very occasionally was a rabbit seen; the few that were positively identified were all *Sylvilagus palustris*, but it is entirely likely that the cotton-tail (*S. floridanus*) is present also. Coues (1871) records one specimen from Shackleford Banks, "the only one I ever saw in the vicinity [of Beaufort]."

Of the chipmunk (*Tamias striatus*), Coues and Yarrow (1878) state: "very common on islands and mainland" in the vicinity of Fort Macon [Bogue Banks], N. C. But Howell (1929) says: "Its absence from the lowlands of the Carolinas and Georgia is difficult to explain"; and Brimley (1945) writes: "absent from the coastal plain . . . so far not known from east of Raleigh." Needless to say, I have never found any sign of chipmunks in this vicinity, nor could I find any native who was familiar with them. It seems hardly possible that Coues and Yarrow could have been mistaken; yet if they were not in error, what has happened to this population in the subsequent years?

The absence of muskrats (*Ondatra zibethica*) seems to be a faunal characteristic of the area in general, rather than of the island as such. The southward distribution of muskrats in the Atlantic coastal plain appears to end abruptly in the area lying between Albemarle Sound and the Pamlico river; on the off-shore bars, muskrats do not occur south of Cape Hatteras.

DIFFERENTIATION WITHIN THE FAUNA

The single chicken-snake collected from Shackleford Banks was judged by Dr. Thos. Barbour to represent a distinct geographic race, and has been described as *Elaphe quadrivittata parallela* Barbour and Engels, 1942. The banded water-snake of Shackleford Banks also was considered by him a new race, and has been described as *Natrix sipedon engelsi* Barbour, 1943. However, since the population of immediately adjacent areas is not sufficiently represented in collections to permit comparison, these snakes may indicate regional, rather than insular, differentiation. The banded water-snake, especially, is likely to turn out to be a regional, brackish-water form. (While this

paper was in press, the latter conclusion regarding *N. s. engelsi* was reached by Robertson and Tyson, 1950, on the basis of specimens of *Natrix sipedon* from Shackleford and Core Banks, Ocracoke Island, and Pitt County on the mainland coastal plain.)

A series of *Eumeces inexpectatus* from Shackleford Banks does not differ materially from a series of the same species from Harkers Island (Engels, 1949). Collections of other vertebrate species from the island have not as yet been analyzed.

COMPARISON WITH OCRACOKE ISLAND FAUNA

Shackleford Bank differs, conspicuously in some ways, from Ocracoke Island, another member of the North Carolina "outer banks" lying about 40 miles to the northeast (Engels, 1942). It is now very much closer to the mainland than is Ocracoke, although the present great distance of Ocracoke from the mainland is undoubtedly due to that submergence which drowned the river valleys and produced the large embayments of Pamlico Sound. On the other hand, it is a smaller "target" than Ocracoke, being only $7\frac{1}{2}$ miles long, against about 17 miles for the latter. This apparent disadvantage is offset by the fact that the tides ebbing out of the North River tend to strike against the inner beach of Shackleford Banks, while the currents of the Neuse and Pamlico rivers are largely dissipated in Pamlico Sound and probably do not reach Ocracoke Island. All in all, it would appear that Shackleford Banks ought to be more accessible to terrestrial vertebrates of the mainland than is Ocracoke.

There are some differences in the habitats represented on the two islands. While there are about 180 acres of woodland and thicket-woodland on Shackleford Banks, there are not more than 3 to 5 acres of real woodland on Ocracoke. On the other hand, the sea-oats (*Uniola paniculata* association) form a more extensive cover on Ocracoke Island than on Shackleford, and intermingled with the sea-oats are thickets of wax myrtle, *Xanthoxylum*, and yaupon holly (*dune thickets*, Engels 1942, fig. p. 282); this latter distinctive habitat is entirely lacking on Shackleford Banks.

Numerically, the faunae of the two islands are practically identical, 33 species being definitely known for Ocracoke Island, 34 for Shackleford Banks. The composition of the fauna, however, differs slightly between the two islands; some, but not all, of the differences can be correlated with differences in available habitat.

Amphibians.—Only 1 amphibian (*Bufo w. fowleri*) is known on Ocracoke Island, against 5 (including *B. w. fowleri*) on Shackleford Banks. The absence of *Hyla squirella* and *Gastrophryne carolinensis* from Ocracoke may be correlated with the very small woodland there, although the "marsh thickets" of Ocracoke (Engels 1942, fig. 8 and p. 298) appear to be similar to some of the *Hyla*-inhabited areas on Shackleford Banks. The almost certain absence of *Rana pipiens* from Ocracoke cannot be ascribed to habitat deficiency. It is possible that the spadefoot occurs on Ocracoke, but escaped

47 (3)

our attention; only one individual, an immature, was seen on Shackleford Banks.

Reptiles.—The Shackleford fauna includes 4 lizards, 6 snakes, and 2 turtles; as against 2 lizards, 4 snakes, and 4 turtles on Ocracoke. The two additional lizards on Shackleford Banks are *Anolis* and *Eumeces*. Apparently suitable habitat for the former, but not for the latter, is quite extensive on Ocracoke. One of the snakes on Shackleford Banks (*Rhadinaea*) here reaches its farthest north, hence Ocracoke Island lies outside the normal geographic limits of the species. Three snakes—*Opheodrys*, *Coluber* and *Natrix*—occur on both islands. One of the two additional turtles on Ocracoke, *Chelydra*, may have been overlooked by us on Shackleford Banks; there is one field notebook entry of trails on the bottom of a fresh water pool doubtfully referred to *Chelydra*.

Birds.—There are some striking differences in the avifauna of the two islands. The two lists have 9 species in common, including 4 of the grassland birds (mourning dove, meadowlark, red-wing and boat-tailed grackle), 3 woodland birds (crested flycatcher, Carolina wren, and cuckoo, the latter rare on both), the ubiquitous vulture, and the shore-frequenting fish crow. On the other hand, a similar number of the common breeding birds of Ocracoke Island are conspicuously absent from the Shackleford avifauna (kingbird, barn swallow, mockingbird, brown thrasher, prairie warbler, yellow-throat, English sparrow, seaside sparrow and song sparrow). Shackleford Banks is within the geographic range of 8 of these 9 species—all except the song sparrow occur in the Beaufort area. Of the 8, two certainly do not find habitat on Shackleford Banks (barn swallow and English sparrow); two more may be placed in the same category with considerably less certainty (kingbird and mockingbird). Domestic animals, especially sheep, may be responsible for the absence of the thrasher and the two warblers. As to birds common on Shackleford Banks but absent from Ocracoke, one of them would find very little suitable habitat there (chuck-will's-widow), and one reaches its farthest north in the Beaufort area (painted bunting), Ocracoke being about 45 miles outside the geographic limits of the species. But again, the absence of one of the thicket and thicket-woodland birds (cardinal) from Ocracoke, while it is common on Shackleford, is indeed puzzling, and, at present, unaccountable.

Mammals.—The two islands are alike in the absence of bats, and of native rodents except the rice rat (*Oryzomys*)—even the latter is not definitely known to occur on Ocracoke. *Rattus rattus* is the only mammal occurring on Ocracoke which is absent from Shackleford, where the edificarian habitat is lacking. Of the Shackleford mammals, two do not occur on Ocracoke, opossum and mole. Habitat for the former is greatly restricted in area on Ocracoke. The absence of moles, however, occurring as they do on both Shackleford Banks and Hatteras Island, is a conspicuous example of the erratic nature of animal distribution on islands (cf. also Engels 1942, pp. 300-301).

DISCUSSION

The perhaps chief fact which emerges from all of the above data is the very obvious one that destruction of habitat is accompanied by elimination of the fauna of that habitat, and that paucity of habitats is accompanied by poverty in species' number. The addition of a new habitat (grassland in place of woodland east of Whale Creek Bay) in this case has not compensated for the probable loss of some species of the previous habitat; only one member of the present vertebrate fauna—the meadowlark—may possibly have been added to the community as a result of that change.

The principal loss of species through the great reduction of the woodland would have involved the avifauna. Our list of birds for the adjacent and rather heavily wooded Harkers Island now numbers 37—more than the total for all vertebrates on Shackleford Banks—and this list is, very likely, still incomplete. Every one of these birds must have occurred on Shackleford Banks in its original forested condition. Except for the absence of moles on Harkers Island, and the presence there of red bats, the mammalian fauna of these two islands is identical, so there is little evidence that mammals have suffered serious depletion in numbers of species through the reduction of the forest; apparently native rodents never did reach the islands. However, it is likely that some of the larger mammals (deer, bear, fox) inhabited Shackleford Banks in precolonial or even colonial days. As to reptiles and amphibians it appears likely that they are as well represented on Shackleford Banks now as they ever were.

With the possible exception, then, of birds, of which at least 70 percent of the mainland species probably originally occurred on the island, the vertebrate fauna of Shackleford Banks is composed of a very impoverished segment of the mainland fauna. Habitat deficiency can account for some, but by no means all, of the depauperation; we are left to conclude that many of the mainland forms have failed, simply, to reach the island. Those, apart from birds, that did reach it, had to swim across the sound, or be carried across in or on floating debris.

Instances have been cited above of observations of snakes swimming in the sounds. An interesting case of the wanderings of a large mammal was recited to me by several Harkers Islanders. About 1925 a bear was seen one night by a flounder-fisherman near the old ferry landing on Harkers Island; surprised by the fisherman, the bear made out from the marsh and into the water (The Straits). A few days later, some women picking berries came upon a bear near The Mullet Pond on Shackleford Banks. Within a week, a bear, "in very poor condition," was run down and killed near the light-house wharf at Cape Lookout, Core Banks. This bear must have circled Harkers Island and reached Shackleford Banks by way of The Straits, North River, and Back Sound, a water distance of more than 6 miles. Later, after traversing the length of Shackleford Banks, it had to swim The Drain to reach Core Banks.

Many animals which are carried out from the mainland on flood waters perish in the flood; after the 1933 hurricane, according to one observer, many

dead animals of all kinds were to be seen in the wreckage and debris on the shore of Cape Lookout—horses, cows, pigs and sheep, cats and dogs, opossums, rabbits, and “even snakes!” But it is likely that, occasionally at least, some individuals would reach higher ground on the islands, and survive the perilous journey. Survival undoubtedly would be enhanced for creatures that found themselves adrift on, or better still, within such debris as partly decayed logs, rather than caught up themselves in the water. Three observations pertinent to this point have been made in the Beaufort area, although none were recorded on Shackleford Banks itself.

A “glass-snake” (*Ophisaurus*) was discovered within a piece of 6" x 6" timber lying on a low sandy ridge at the edge of the marsh on Pivers Island, one of the several small islands of Beaufort Harbor. This was within 30 feet of the water's edge, not more than 2 feet above the level of mean high water, and well within the zone of accumulation of drift. Two brown-backed lizards (*Leiolopisma*) were found within a log lying at the inner edge of the marsh of Jane's Creek on Harkers Island. This is a tidal creek which penetrates Harkers Island from the North River. Four yellow-lipped snakes (*Rhadinaea*) were found within another log at the inner edge of the Jane's Creek marsh. There can be little doubt but that these logs were deposited, where we found them, by flood waters. It is not suggested that these particular individuals reached the islands in the logs and the timber in which they were discovered (although, for *Leiolopisma*, these are our only records for the outer banks), but they indicate a mode of dispersal whereby islands could be invaded, either from the mainland or from other islands. Species whose habits would favor such accidental transport, within partly decayed logs, include two of the five amphibians found on Shackleford Banks, *Gastrophryne* and *Hyla squirella*, two of the lizards, *Ophisaurus* and *Eumeces*, and a snake (*Rhadinaea*). “The accident of transshipment on beach drift” was considered by Hatt *et al.* (1948, pp. 141-143) one of the more important factors in determining the composition of insular faunas in Lake Michigan; Jackson (1920) concluded that the mammalian fauna of the Apostle Islands in Lake Superior was composed of animals that were active in winter, or were strong swimmers, or were frequently found in driftwood on the beach. Winter activity hardly takes part in populating the North Carolina outer banks because the sounds remain open in winter; but it may be pointed out that in 1917, Back Sound and Core Sound were solidly frozen over for a period of about 10 days, and a similar “big freeze” is recalled by some of the older natives as having occurred “65-75 years ago.”

SUMMARY

Shackleford Banks is an off-shore bar, submarine in origin, hence its fauna and flora were acquired, subsequent to its emergence, through over-water invasion. The island is about 8 miles long, $\frac{1}{4}$ to $\frac{1}{2}$ miles wide; it lies 2 to 5 miles off the mainland coast of North Carolina. In form and general topography it is a typical barrier-beach island but it has suffered drastic changes in its vegetational cover, and in its form, in the past half-century. It was former-

ly wooded in its entire length; this woodland, covering about 1250 acres, probably was composed chiefly of live oak, red cedar, yaupon holly and loblolly pine. The inner shore, on the eastward half of the island, was bordered by salt marshes; the only other grassland consisted of the sea-oats covering the dunes back of the outer beach. Due largely, as this writer believes, to naturally initiated erosion of the outer beach, to hurricane floods, and to drifting sand, the woodland has been reduced to approximately 180 acres, about 15 percent of its original area. It has disappeared entirely from the eastward half of the island, where it has been replaced by grassland; some of the salt marsh has also been converted into a dry grassland through the deposition of wind-borne sand from the outer beach. On the westward half of the island, where generally higher elevations occur (10 to 20 feet), a sand wall is advancing across the island, and burying the woodland. Here the outer half of the island has been converted into a barren, sandy wasteland, on which stand the skeletons of red cedars. Between the sand wall and the inner beach, in a strip about $2\frac{1}{2}$ miles long and 180 to 400 yards wide, stands the remnant of the woods and thicket-woodland, occasionally intersected by marshes extending in from the inner beach. There are now probably no permanent fresh-water pools on the island. In September, 1933, a hurricane flood cut a new inlet across its eastern end, separating Shackleford Banks from Core Banks and Cape Lookout. The island has been uninhabited for some years, although formerly it supported a small population of fishermen; it has a relatively large population of semi-feral sheep, goats, pigs, cattle and horses.

Shackleford Banks has a moderately temperate climate, with an average continuously frost-free season of 269 days. Tropical storms of hurricane intensity hit in upon, or pass close by, the North Carolina coast with an average frequency of 1 every 4 years. Since 1879, two of these, because of their intensity and diameter, were classed as "great" hurricanes; they occurred in August 1885 and September 1933.

At least 34, and probably not more than 40, species of land vertebrates—exclusive of shore- and aquatic-birds—occur on this island, as against about 186 species on the adjacent mainland. Only about 15 percent of the amphibians of the mainland occur on the island, not more than 20 percent of the land birds (perhaps only 15 percent), and about 25 percent of the reptiles and mammals.

The amphibian fauna consists of five frogs and toads, representing 5 anuran families; salamanders appear to be absent from the fauna. There are 4 lizards, at least 6 snakes, and at least 2 turtles. Conspicuous, definitely determined absentees include the oak-toad (*B. quercicus*), and poisonous snakes of the genera *Crotalus* and *Agkistrodon*; only one blue-tailed skink (*Eumeces*), of the three species occurring in the coastal plain, has reached the island. One of the snakes (*Rhadinaea*) here reaches its northernmost limit of distribution.

Apparently only 12, but perhaps 16, species of land birds breed on the island; of these, only 8 occur in considerable numbers, 4 of these species being primarily grassland birds, and 4 belonging to the thicket-woodland. One of

the latter (painted bunting) here reaches its northernmost limit of distribution. Conspicuous absentees include warblers, mimids, the towhee, and the seaside sparrow, all of which occur in numbers on adjacent islands.

There are definitely 5, possibly 7, species of mammals in the fauna. Conspicuous absentees are all native rats and mice except the rice-rat (*Oryzomys*)—indeed all rodents except the rice-rat, house-mouse and marsh-rabbit—and all bats. A mole (*Scalopus*) occurs, although it is absent from nearby Harkers Island.

Some of the apparent depauperation of the vertebrate fauna almost certainly is due to lack of diversity of habitat, but this factor alone does not account for all of the absentees. The destruction of the woodland probably affected primarily the avian fauna—about 3 times as many birds occur on nearby, relatively heavily wooded Harkers Island. Some of the larger mammals—deer, bear, fox—probably originally occurred on the island, as well as the red bat. Amphibians, lizards and turtles were probably not materially reduced in numbers of species by the almost total disappearance of the woodland. The replacement of woodland by grassland probably did not add more than one species (meadowlark) to the fauna.

Two of the 5 amphibians, 2 of the 4 lizards, and one of the snakes most likely reached the island within partly decayed logs carried by flood waters.

REFERENCES

- AMERICAN ORNITHOLOGISTS' UNION 1931—Check list of North American birds. 4th edition—Lancaster, Pa.
- BARBOUR, T. 1943—A new water snake from North Carolina. *Proc. New England Zool. Club* 22: 1-2.
- AND W. L. ENGELS 1942—Two interesting new snakes. *Ibid.* 20: 101-104.
- BRIMLEY, C. S. 1942—The amphibians and reptiles of North Carolina. No. 22. Carolina Biol. Supply Co. (Elon College, N. C.), *Carolina Tips* 5(1): 3.
- 1945—The mammals of North Carolina. No. 9. *Ibid.* 8(1): 3.
- BURLEIGH, T. D. 1937—Bird life on the North Carolina coast. *The Auk* 54: 452-460.
- COUES, E. 1871—Notes on the natural history of Fort Macon, N. C. and vicinity. No. 1. (Mammals, birds, and reptiles). *Proc. Acad. Nat. Sci. Phila.* 1871: 12-49.
- AND H. C. YARROW 1878—Notes on the natural history of Fort Macon, N. C. and vicinity. No. 4 (Supplement to No. 1: additional notes on mammals, birds and reptiles; amphibia). *Ibid.* 1878: 21-28.
- ENGELS, W. L. 1942—Vertebrate fauna of North Carolina coastal islands. I. Ocracoke Island. *Amer. Midl. Nat.* 28: 273-304.
- 1949a—Crested flycatchers nesting some distance from their foraging areas. *The Auk* 66: 287-288.
- 1949b—The blue-tailed skinks (*Eumeces*) of two North Carolina coastal islands. *Copeia* 1949: 269-271.
- FIATT, R. T., J. VAN TYNE ET AL. 1948—Island life: a study of the land vertebrates of the islands of eastern Lake Michigan. *Bull. no. 27, Cranbrook Instit. Sci.* xi+179 pp. Bloomfield Hills, Mich.
- HOWELL, A. H. 1929—Revision of the American chipmunks (genera *Tamias* and *Eutamias*). U. S. Dept. Agric., *Bur. Biol. Surv., North American Fauna* No. 52.

- JACKSON, H. H. T. 1920—An apparent effect of winter inactivity upon distribution of mammals. *Journ. Mammalogy* 1: 58-64.
- JOHNSON, D. W. 1919—Shore processes and shoreline development. Chapters vii-viii. New York: John Wiley and Sons.
- LEWIS, I. F. 1917—The vegetation of Shackleford Bank. North Carolina Geological and Economic Survey, Economic paper no. 46, pp. 1-40. Raleigh, N. C.
- MILLER, G. S. JR. 1924—List of North American Recent mammals, 1923. *U. S. Nat. Mus. Bull.* 128. xvi+1-673 pp.
- ROBERTSON, W. B. AND E. L. TYSON 1950—Herpetological notes from eastern North Carolina. *Jour. Elisha Mitchell Sci. Soc.* 66: 130-147.
- STEJNEGER, L. AND T. BARBOUR 1943—A check list of North American amphibians and reptiles. 5th Edition. *Bull. Harvard Mus. Comp. Zool.* 93(1): 1-260.
- TANNEHILL, I. R. 1944—Hurricanes, their nature and history. 5th Ed. x+269 pp., 121 figs. Princeton, N. J., Princeton Univ. Press.
- U. S. WEATHER BUREAU 1933—Climatic summary of the United States. Climatic data herein from the establishment of stations to 1930, inclusive. R. J. Martin, Editor. Section 97—Northeastern North Carolina. 15 pp.
- WELCH, W. L. 1885—An account of the cutting through of Hatteras Inlet, North Carolina, September 7, 1846. *Bull. Essex Instit.* 17. (Reprinted, Salem: Salem Press. 13 pp.)

The Genus *Orconectes* in Louisiana (Decapoda, Astacidae)

George Henry Penn

Department of Zoology, the Tulane University of Louisiana, New Orleans

This is the second of a series of four papers on the crawfishes of Louisiana; the first, on the genus *Cambarellus*, appeared in this journal (Penn, 1950b), which see for introductory remarks. Many of the specimens on which these studies are based have since been placed in other collections. Abbreviations for these are as follows: AMNH = American Museum of Natural History, ANS = Academy of Natural Sciences of Philadelphia, HHH = Horton H. Hobbs, Jr. personal collection, INHS = Illinois Natural History Survey, LSU = Louisiana State University, MCZ = Museum of Comparative Zoology at Harvard University, TU = Tulane University (Department of Zoology), UMMZ = University of Michigan Museum of Zoology, and USNM = United States National Museum.

Genus *ORCONECTES* Cope, 1872

Diagnosis.—First pleopod of form I male terminating in two distinct parts only, both ending in straight or gently curved, short or long spines or blade-like processes. There is never a strongly developed shoulder on the distal cephalic margin of the pleopod. In the male hooks are present on the ischiopodites of the third, or third and fourth pereopods.

The genus is divided into two subgenera, both of which occur in Louisiana.

Subgenus *ORCONECTES* Cope, 1872

Diagnosis.—Terminal processes of form I male more or less equal in length; both either long or short, straight or gently curved. Rostrum with or without lateral spines; areola open or obliterated. In the male hooks are present on the ischiopodites of the third, or third and fourth pereopods.

Three species are known to occur in Louisiana.

ORCONECTES (ORCONECTES) LANCIFER (Hagen)

Cambarus lancifer Hagen, 1870, Ill. Cat. MCZ 3: 59; *Cambarus faxonii* Meek, 1894, Amer. Nat. 28: 1042; *Faxonius lancifer* (Hagen) Penn, 1939, Amer. Midl. Nat. 22: 215; *Orconectes lancifer* (Hagen) Hobbs, 1942, Amer. Midl. Nat. 28: 350.

Diagnosis.—Rostrum with lateral spines; rostrum and antennal scales decidedly elongate; areola obliterated; hooks on ischiopodites of third pereopods only. The two rami of first pleopod of form I male short and recurved; central projection blade-like.

Type locality.—"Root Pond, Mississippi" according to Hagen (1870), corrected to "Tallahatchie River at Rocky Ford, near the town of Etta, Union County, Mississippi" by Penn (1939); type, MCZ 306.

Specimens examined.—Previously recorded only from Mississippi, Arkansas and Ten-

nessee. From Louisiana I have seen only twenty specimens and have records of a few others from the following localities arranged by parishes: ASCENSION: Bayou Manchac at Hope Villa, X-9-36, (TU P. 757); EAST BATON ROUGE: Baton Rouge (LSU); INERIA: Bayou Teche, $\frac{1}{2}$ mi. e. Daspit, IV-9-49 (TU 1042); NATCHITOCHEs: Black Lake, 2 mi. s. Creston, VIII-7-49 (TU 1470), Cane River Lake near Bermuda, XI-12-28 (USNM), 8 mi. n. Derry, VII-15-31 (UMMZ); OUACHITA: Ouachita River near Monroe, VIII-21-37 (TU P. 422), J. A. Noe Fish Hatchery, 7 mi. n. Monroe, II-14-41 (MCZ, HHH, TU P. 480); POINTE COUPEE: False River, IX-10-24 (TU P. 827); RAPIDES: tributary to Bayou Rapides, 5 mi. w. Alexandria, VIII-1-49 (TU 1355); ST. TAMMANY: creek tributary to Pearl River at Talisheek, II-9-39 (TU P. 539); TANGIPAHOA: Bedico Creek, 4 mi. e. Ponchatoula Beach, VIII-12-48 (TU 758).

Life history.—With so few specimens from Louisiana and elsewhere it is not possible at the present to give much data on the life history of *O. lancifer*. Although we have collections made in February, April, August, September, October and November, form I males have not been seen in Louisiana. However, Mr. Percy Viosca, Jr. collected a number of females carrying eggs in February; some of these have been placed in the Tulane collection (TU P. 480). Apparently the type specimen, which was probably collected in April (Penn, 1939) is the only form I male known. A collection from Reelfoot Lake, Tennessee in July were all immature (Hobbs and Marchand, 1943); other published records do not include form I males nor are dates of collections given (Meek, 1894; Faxon, 1898).

Ecological observations.—Although only ten lots of *O. lancifer* are represented by more or less complete ecological data, it appears that this species is confined to more or less permanent and large bodies of water. These habitats in Louisiana were slow-flowing bayous (30%), rapid-flowing creeks and rivers (30%), lakes (30%) and ponds (10%). An analysis of the various physical and biological factors affecting all habitats recorded may be summarized in the statement that *O. lancifer* occurs most frequently in deep water, i.e., more than 15 inches deep (90%), which is clear (60%), permanent (100%), either flowing or static (50% each), and exposed to full sunlight (100%). Most of the lots were from habitats with mud or mud and sand bottoms (80%) and with little or no aquatic vegetation present (40%). The few aquatic plants found in these habitats, in order of their occurrence, were *Lemma* spp., *Ceratophyllum* spp., *Najas* sp., and *Jussiaea* sp.

ORCONECTES (ORCONECTES) PALMERI CREOLANUS (Creaser)

Faxonius creolanus Creaser, 1933, Occ. Pap. Mus. Zool. Univ. Mich. 275: 16; *Orconectes creolanus* (Creaser) Hobbs, 1942, Amer. Midl. Nat. 28: 352.

Diagnosis.—Rostrum with lateral spines; rostrum and antennal scale of moderate length; areola obliterated; hooks on ischiopodites of third pereopods only in form I males. Both rami of first pleopod of form I male setiform, the mesial process swollen, just proximad of tip, trough-like and recurved; quotient of first pleopod length into length of cephalothorax greater than 3.00.

Relationships.—On the basis of a preliminary comparative study of a series of *creolanus* from Louisiana (including Creaser's specimens) and a series of *palmeri* from Tennessee, Arkansas and Missouri within a short radius of the

type locality I have considered *creolanus* to be a subspecies of *palmeri*, differing primarily in the relative lengths of the first pleopods of the males (both form I and II).

Type locality.—"Stream tributary to the Amite River, one-half mile north of Ethel, East Feliciana Parish, Louisiana"; holotype: UMMZ 53332

Specimens examined.—From Louisiana I have seen 88 specimens from the following localities arranged by parishes: CLAIBORNE: spillway ditch below Corney Lake, 4.5 mi. se. Scottsville, VI-29-50 (TU 2146); FRANKLIN: Bayou Macon at Como, VI-25-37 (TU P. 626); GRANT: Big Creek at Fishville, VII-20-37 (TU P. 563), same locality, VI-26-47 (TU 78), Pollock, July-Aug., 1941 (USNM); MADISON: Tensas River, 2 mi. s. Quebec, X-16-36 (TU P. 613); OUACHITA: Ouachita River at Monroe, VIII-21-37 (TU P. 422); ST. LANDRY: Bayou Carron at Washington, VI-23-48 (HHH, TU 417); ST. TAMMANY: Abita River at Abita Springs, VI-3-37 (TU P. 625).

In addition to these new localities, *O. palmeri creolanus* has been recorded from the following localities in Louisiana by Creaser (1933): EAST FELICIANA: the type locality; LA SALLE: tributary to Little River at Jena (UMMZ); and GRANT: tributary to Little River at Pollock (UMMZ).

Life history.—At present it is not possible to make a statement on the life history of this species. Only two form I males have been recorded: one June 23, 1948 (TU 417) and the other July 17, 1931 (Creaser, 1933). Ovigerous females are unknown.

Ecological observations.—Only several collections bear ecological data so that only a few tentative statements may be made. Habitats recorded are: rapid-flowing creeks and rivers (70%), slow-flowing bayous (20%), flowing ditch below impounded lake (10%). Of these all were permanent, and an equal number each had mud and sand bottoms.

ORCONECTES (ORCONECTES) HOBBSI Penn

Orconectes (Orconectes) hobbsi Penn, 1950, J. Wash. Acad. Sci. 40: 381.

Diagnosis.—Rostrum with prominent lateral spines, upper surface deeply concave; areola very narrow, almost closed. Males with hooks on ischiopodites of third pereopods only. First pleopod of form I male terminating in two long, setiform, deeply split rami; central projection recurved at a right angle to the shaft, mesial process trough-like just proximad of the apex and recurved at about right angles to the shaft. Quotient of cephalothorax length divided by length of first pleopod less than 3.00.

Type locality.—"Headwater creek of Bayou Lacombe, at St. Tammany, 6 mi. n. Lacombe, St. Tammany Parish, Louisiana"; holotype: USNM 90952.

Specimens examined.—I have seen 65 specimens from Louisiana, all of which were included in the paratype series. Paratypes were recorded from East Feliciana, Livingston, St. Helena and St. Tammany parishes in Louisiana in addition to Amite and Pike counties in Mississippi (Penn, 1950c).

Life history.—Comparatively little can be written other than that form I males have been taken only in the winter months (November and January), that juvenile males and females are rather abundant in mid-summer (June-July), and that ovigerous females have never been collected.

Ecological observations.—Although only eleven lots of *O. hobbsi* bear

more or less detailed ecological data these show a close similarity. All collections were from rapid-flowing creeks (82%) and rivers (18%). Of these, most were in deep water, i.e. more than 15 inches deep (55%), which was clear (100%), permanent (100%), shaded (80%), with sandy bottoms (91%), and without aquatic vegetation (70%).

Subgenus FAXONELLA Creaser, 1933

Diagnosis.—Pleopods of form I male terminating in two rami: the central projection at least twice the length of the mesial process. Male with hooks on ischiopodites of third pereopods only. Rostrum without lateral spines and barely a trace of an acumen, upper surface slightly excavate; areola broad. Chelae with inflated subcylindrical palm; fingers about equal in length to the palm.

Only two species known, both of which occur in Louisiana.

ORCONECTES (FAXONELLA) CLYPEATUS (Hay)

Cambarus clypeatus Hay, 1899, Proc. U. S. Nat. Mus. 22: 122; *Faxonius (Faxonella) clypeatus* (Hay) Creaser, 1933, Occ. Pap. Mus. Zool. Univ. Mich. 275: 19; *Orconectes clypeatus* (Hay) Hobbs, 1942, Amer. Midl. Nat. 28: 352.

Diagnosis.—First pleopod of form I male reaching coxopodite of first pereopod; central projection very long, slender, subcylindrical and corneous, mesial process very short (between one-third and one-half length of central projection), acute and non-corneous; the two pleopods overlap apically in their normal positions.

Type locality.—"Bay Saint Louis, Hancock County, Miss. (found in a skiff)"; type USNM 22778.

Specimens examined.—This is one of the commonest crawfishes in Louisiana and I have examined well over 1,500 specimens from localities in 27 of the 64 parishes of the state, as follows: ALLEN: Elizabeth (TU P. 587); BOSSIER: Arcana (TU 1777), 5 mi. e. Benton (TU 1778), 4 mi. ne. Midway (MCZ); 4 mi. ne. Plain Dealing (TU 1422); CADDO: Rodessa (TU 1409); CALCASIEU: DeQuincy (INHS), Lucas (TU P. 531); CALDWELL: 4 mi. e. Columbia (TU 430); CAMERON: Ferrell (TU P. 537); CLAIBORNE: 8 mi. e. Lisbon (TU 1456); EAST FELICIANA: Clinton (MCZ) Nesom (TU P. 544); EVANGELINE: 4 mi. e. Bayou Chicot (TU 1570), Beaver (UMMZ), near Chicot State Park (TU 497), Pine Prairie (HHH), Turkey Creek (USNM); FRANKLIN: 2 mi. sw. Como (TU 1873), 3 mi. e. Winnsboro (TU 1870); GRANT: near Dry Prong (HHH), Fishville (AMNH), 1 mi. s. Magnolia Park (TU 1769), 5 mi. se. Verda (ANS), 7½ mi. n. Williana (TU 1834); JACKSON: 1 mi. s. Womack (AMNH), 1 mi. n. Wyatt (TU 72); LA SALLE: 2 mi. e. Summerville (TU 2141); LINCOLN: 3 mi. nw. Downs ville (TU 1858), 3 mi. se. Ruson (USNM); LIVINGSTON: Denham Springs (AMNH, TU P. 549), Port Vincent (INHS); MOREHOUSE: 5 mi. e. Bastrop (HHH), Bayou Bartholomew (TU P. 535), Galion (INHS); NATCHITOCHES: Chestnut (USNM), 4 mi. s. Derry (MCZ), Kisatchie (TU P. 578); OUACHITA: Eureka (TU 1856), 1 mi. s. Perryville (TU 1864), 2 mi. se. Pine Grove (TU 1866); RAPIDES: near Hineston (TU 1058); RICHLAND: 6.5 mi. w. Alto (TU 1868); ST. HELENA: Montpelier (UMMZ), Pine Grove (USNM, TU P. 540); ST. TAMMANY: 1 mi. n. Bonfouca (TU 147), 2 mi. w. Bush (MCZ), Covington (TU 1901), 4 mi. w. Covington (USNM), 4 mi. ne. Covington (TU 729), Florenville (TU 142, 143), 4

mi. w. Florenville (TU 459), Goodbee (UMMZ), Hickory (HHH, AMNH, TU P. 564, 181, 197, 198, 300, 880, 895, 945, 1500), Hygea (TU P. 561), Mandeville (AMNH, TU P. 628), Pearl River (ANS, MCZ, TU P. 560, P. 619, 878, 896, 967), Slidell (AMNH, TU 968), 5 mi. w. Slidell (INHS), St. Tammany (HHH, UMMZ, TU 145, 1900), Sun (USNM, TU P. 825), Talisheek (ANS, USNM), 4 mi. w. Talisheek (TU 737), 2½ mi. s. Talisheek (TU 2023); TANGIPAHOA: 3 mi. e. Amite (TU 222), 3 mi. e. Ponchatoula Beach (HHH), 4 mi. w. Tangipahoa (UMMZ), 1 mi. w. Tickfaw (USNM, INHS); VERNON: near Hicks (UMMZ), near Leesville (TU 498), Pitkin (ANS); WASHINGTON: Sheridan (TU 182); WEBSTER: near Caney Lake (ANS), Shongaloo (TU 1776); WINN: 2 mi. ne. Gaars Mills (TU 1839).

In addition to these new records *O. clypeatus* has been recorded previously from Louisiana as follows: GRANT: 3.4 mi. s. Selma (Creaser, 1933); RAPIDES: near Forest Hill, introduced (Penn, 1942); ST. TAMMANY: Pearl River (Penn, 1942).

Life history.—Very little of significance has been recorded to date and ovigerous females have never been reported. The life cycle is a very unique and interesting one and will be reported on at an early date by Miss Elsie Wayne Smith, a graduate student at Tulane University. Miss Smith is completing an excellent statistical population and life history analysis of *Orconectes clypeatus* in southeastern Louisiana.

Ecological observations.—An analysis of the 81 lots of *O. clypeatus* on which we have more or less complete habitat data is summarized briefly in the table below:

Habitat	Percent of total collections
TEMPORARY SITUATIONS	58.1%
Ditches (mostly roadside)	26.0
Pineland sloughs	13.6
Puddles and borrow pits	7.4
Potholes in dry creek beds	6.2
Burrows	4.9
PERMANENT SITUATIONS	41.9%
Ponds	18.5
Creek and rivers	14.8
Swamps and swamp-ponds or pools	8.6

An analysis of the various physical and biological factors obtaining in all habitats may be summarized in the statement that *O. clypeatus* occurs most frequently in shallow water, i.e. less than 15 inches deep (84.6%), which is clear (64.5%), temporary (58.1%), static (77.0%), and exposed to full sunlight (70.6%). Most of the collections were from habitats with mud bottoms (67.7%) and with aquatic plants present (72.5%). The aquatic plants most commonly found in these places, in order of their frequency, were: *Polygonum* spp., *Juncus* spp., *Nuphar* sp., *Myriophyllum* sp., *Eleocharis* sp., *Persicaria*

sp., *Bramia monnieri*, *Jussiaea* spp., *Ceratophyllum* spp., *Potamogeton* spp., *Proserpinaca* sp., *Achyranthes philoxeroides*, *Tradescantia* sp. and *Scirpus* sp.

ORCONECTES (FAXONELLA) BEYERI Penn

Orconectes (Faxonella) beyeri Penn, 1950, J. Wash. Acad. Sci. 40: 166.

Diagnosis.—First pleopod of form I male reaching coxopodite of third pereopod; central projection a long, flattened, somewhat sickle-shaped process bent mesially; mesial process much shorter, less than half the length of the central projection, bent in same direction; the two pleopods overlap each other in normal position.

Type locality.—"Roadside ditch, 2 mi. ne. Naborton, DeSoto parish, Louisiana"; holotype: UHNM 90361.

Specimens examined.—This species is known only by twelve specimens from two localities, both in Louisiana as follows: DE SOTO: 2 mi. ne. Naborton, VIII-5-49 (USNM, TU 1440); NATCHITOCHEs: near Ajax, V-22-49 (HHH, TU 1227).

Life history and Ecological observations.—It is probable that the life history of *O. beyeri* closely parallels that of *O. clypeatus* in Louisiana, but I have no data other than on these two collections. Form I males were present in August but not in May.

We have habitat data for only the collection from DeSoto parish. Here they were found in an "unshaded, mud-bottomed ditch in which the water was less than 12 inches deep, amber-colored and slightly turbid. Aquatic plants including *Jussiaea* sp. were present, indicating the probability that the habitat is at least semipermanently wet" (Penn, 1950a).

REFERENCES

- CREASER, EDWIN P. 1933—Descriptions of some new and poorly known species of North American crayfishes. Occ. Pap. Mus. Zool. Univ. Mich. No. 275: 1-21.
- FAXON, WALTER 1898—Observations on the Astacidae in the United States National Museum and in the Museum of Comparative Zoology, with descriptions of new species. Proc. U. S. Nat. Mus. 20: 643-694.
- HOBBS, HORTON H. JR. AND LEWIS J. MARCHAND 1943—A contribution toward a knowledge of the crayfishes of the Reelfoot Lake area. J. Tenn. Acad. Sci. 18(1): 6-35.
- MEEK, S. E. 1894—A new *Cambarus* from Arkansas. Amer. Nat. 28(336): 1042-1043.
- PENN, GEORGE HENRY 1939—The type locality of the crawfish (*Faxonius lancifer*). Amer. Midl. Nat. 22(1): 215.
- 1942—Observations on the biology of the dwarf crawfish, *Cambarellus shufeldtii* (Faxon). Ibid. 28(3): 644-647.
- 1950a—A new crawfish of the genus *Orconectes* from Louisiana. J. Wash. Acad. Sci. 40(5): 166-169.
- 1950b—The genus *Cambarellus* in Louisiana. Amer. Midl. Nat. 44(2): 421-426.
- 1950c—A new *Orconectes* from the Pontchartrain watershed in Louisiana and Mississippi. J. Wash. Acad. Sci. 40(11): 381-384.

Some Influences of the American Hookworm^{1,2}

James E. Ackert

Kansas State College, Manhattan

The term *American hookworm* is an adopted name for a parasite of the African natives that were brought to the Louisiana territory in the latter part of the 18th century. Hookworms first came into prominence in the early 1870's when the St. Gotthard Tunnel was being dug through the Alps Mountains. Workers suffered with a form of itch from penetrating hookworm larvae in the ever present mud. Many such infected workers left the tunnel and went to mines in Germany, where hookworms were seen in 1890 by an American Zoologist, Dr. Charles W. Stiles, who was studying in Leipzig.

On Stiles' return to the United States in 1892, he lectured to medical students in the vicinity of Washington and cautioned them to be on the lookout for hookworms in the tropics or subtropics in cases of anemia in which the cause was not clear (Stiles, 1939). Later, one of the army medical students, Dr. Bailey K. Ashford, who had been sent to Puerto Rico, collected some hookworms from hospital patients which he, in 1900, determined to be the Old World hookworm, *Ancylostoma duodenale*. Soon afterward some hookworms from a Southern patient were examined by Stiles and found to be markedly unlike the Old World hookworm.

It was to review briefly the importance of this hookworm, which is scarcely a half-inch in length, and to elaborate upon influences emanating from its presence in the Southern United States, that this paper was prepared.

STILES ANNOUNCES NEW HOOKWORM

Early in 1902, hookworms which had been found in Texas were determined by Stiles to be a new species to which he gave the name *Necator americanus*. Stiles' announcement of the newly discovered American hookworm, made at a medical meeting in Washington on May 10, 1902, was followed by a trip to nearby Virginia, and to North and South Carolina to look for hookworms. To his astonishment he found hookworms in each state. They were of the new species, and so numerous that hookworm disease appeared to be one of the most important ailments in that portion of the South, especially on farms and plantations. He stated (1902), "indications are not entirely lacking that much of the trouble popularly attributed to 'dirt-eating,' 'resin-chewing,' and even some of the proverbial laziness of the poorer classes of the white population are in reality various manifestations of uncinariasis" (hookworm disease).

The next month, Dr. H. F. Harris,³ who was studying malaria in Georgia

1 Address of the Guest Speaker, Third Annual Mid-Western Conference of Parasitologists, June 18, 1951, Purdue University, Lafayette, Indiana.

2 Contribution No. 287 from the Department of Zoology, Agricultural Experiment Station, Kansas State College of Agriculture and Applied Science, Manhattan, Kansas.

3 State Health Officer, Georgia, 1902.

and Florida, found evidence that the widespread anemia was due not to malaria but to hookworms, and also that this was the most common of the serious diseases in Georgia, Florida and Alabama.

LIFE CYCLE AND FEEDING HABITS OF HOOKWORMS

While the life cycle of the hookworm was not known at that time, it had been determined that a mode of entrance into the human body was by penetration of hookworm larvae from the soil through the skin, which accounted for the term "ground itch." Doctors, unaware of the cause of such itch, had been treating it externally for years.

Details of the life of the larvae in the soil and of their migratory course through the human body to the lungs and eventually to the small intestine soon were elucidated; but perhaps the most damaging feature of hookworm parasitism came to light in 1931 when Wells discovered that hookworms after lacerating the wall of the intestine and injecting an anticoagulin into the wound, take blood far in excess of their nutritional needs. It was determined by Foster and Landsberg (1934) that the anemia produced by these hookworms can be accounted for solely by the volume of host blood lost.

STILES SEEKS MASS ATTACK ON HOOKWORMS

Late in 1902, Stiles, who had been employed by the U.S. Public Health Service, was requested by Surgeon General Walter Wyman to present his findings from the Southern trip to an international public health meeting at Washington, D.C. A newspaper correspondent covering the meeting was struck by the symptoms described, and reported in the New York papers that the U.S. Public Health Service had discovered the "germ of laziness." This report which was telegraphed throughout the world brought some ridicule upon Stiles, but it did more in a few days to spread knowledge of hookworm disease than purely scientific articles would in a decade.

Convinced of the importance of his discovery, Stiles lectured to medical groups and institutions. His audiences learned of various hookworm effects such as weakness, foot and leg ulcers, stunted growth (Figs. 1, 2), retarded mental development, anemia and suspension of menstruation (Stiles, 1910). Stiles also cited evidence that hookworm disease impedes recovery from tuberculosis. The chances for death from this disease are about doubled in hookworm cases (Stiles, 1909).

While progress was being made in bringing the problem of hookworm disease to the attention of the State medical associations and some doctors were able to diagnose the disease, it was apparent that this health menace would continue for decades unless funds were made available for a large scale field attack. Thereupon, Stiles and Surgeon General Walter Wyman sought financial assistance from Congress, but legal complications in connection with appropriations prevented active field work for eradication.

A ray of hope appeared when in a conference of various medical men one evening early in 1908 at the Washington, D.C., Cosmos Club, arrangements were made for a very large endowment under the condition that the name of

the donor remain secret.⁴ At this time, Stiles had been called to President Theodore Roosevelt's Country Life Commission. As the Commission proceeded by rail, Stiles was chatting with Walter Hines Page, another Commission member, when the morning papers became available. To Stiles' astonishment he saw the headlines announcing the death of the donor of the heavy endowment. Stiles feeling ill, informed Page of the loss of the endowment; whereupon, Page remarked that fortunately this gentleman was not the only rich person in the country (Stiles, 1939).

To appreciate the part Page played in hookworm eradication and in other phases of this study it is necessary to review briefly some of his convictions and activities. A native of North Carolina, he was trained in its public schools, an academy and in Trinity College (forerunner of Duke University), before he was chosen in 1876 as one of 20 brilliant young men for the graduate student body of the newly founded Johns Hopkins University. His advanced studies in English and Greek led him into journalism. In a few years he went from reporter to editor in a series of positions in the East, North, and Middle-West, and on to his own South where in Raleigh, North Carolina, he founded the *State Chronicle* to uplift the backward masses still floundering since the close of the Civil War. Better farming, better schooling, further development of natural resources, and regained manufacturing industries were among the subjects he treated.

Although Page's efforts appealed to many in the South, popular support at the time was not sufficient to continue his *Chronicle*. He then went North and soon settled into highly successful journalistic work, editing in succession the *Forum* and *Atlantic Monthly* and then founding the notable *World's Work*.

Twelve years later Page was invited to return and address the North Carolina State Normal College for Women. He disparaged the low living standards, stating that "one out of every four was a 'Forgotten Man' unable to read or write." Page lectured informally, but with great force. "Even more tragic than these 'Forgotten Men,'" he stated, "were the 'Forgotten Women'; thin and wrinkled in youth from ill-prepared food, clad without warmth, or grace, living in untidy houses, working from daylight till bedtime at the dull round of weary duties, the slaves of men of equal slovenliness, the mothers of joyless children—all uneducated if not illiterate." "This sight," Page told his hearers, "every one of you has seen. . . ."

Returning to New York, Page continued to speak and write on his favorite subject. Articles were published year after year in the *World's Work*, the *Atlantic*, and the *Outlook*, and in such leading newspapers as the *Boston Transcript*, the *New York Times*, and the *Kansas City Star* (Hendrick, 1924).

Such were the convictions and activities of Page in his efforts to uplift the backward masses in the South in 1908, when he was chosen as a member of

⁴ Charles W. Stiles. Memorandum. Early history of hookworm in America, February 10, 1923.

President Theodore Roosevelt's Country Life Commission. Stiles' mission also concerned the South. He wanted to obtain an endowment sufficient to rid the South of the hookworm which sapped the blood and energy of the rural people, leaving them underdeveloped physically and mentally. Page became an attentive listener; the more facts presented by Stiles, the more impressed Page became, until he was converted and zealously so. The hookworm now filled his mind. "How much Southern history did the thing explain? Was it forces like this that really controlled the destinies of mankind?" Page saw his North Carolinians as being ill with hookworm. Free them from this energy-consuming parasite and a new generation would result.

Page now joined Stiles in the quest for a large grant. Wanting to reach John D. Rockefeller; Page laid the hookworm case before his close friend Secretary Walter Buttrick of the General Education Board. Buttrick was impressed and approached Frederick T. Gates, Rockefeller representative, who after some delay obtained one million dollars from Rockefeller to combat this devitalizing pest. The bequest, which was given for a five-year period (1909-1914), was administered by the newly formed Rockefeller Sanitary Commission for the Eradication of Hookworm Disease. The Commission included Page as a member, Wycliffe Rose as administrative secretary, and Stiles as scientific secretary.

THE ROCKEFELLER SANITARY COMMISSION FOR THE ERADICATION OF HOOKWORM DISEASE

Early in 1910 the Commission began by making the State the unit of organization and work, because each state had its own system of public health, of organized medicine, of public press, and its own system of public schools and minor agencies for educating the people. By cooperating with these existing agencies, which were rooted in the life and traditions of the population, benefits of the undertaking were likely to remain permanent. No state was entered without invitation from the State Board of Health. This body in cooperation with the Commission chose a State Director of Sanitation as head of the eradication work in his state. By the end of the first year nine Southern states had sent invitations to the Commission, had their Sanitary Directors approved, and the work inaugurated.

The field work was done by a group of sanitary inspectors who determined the geographic distribution, degree of infection, and the sanitary conditions responsible for the presence and spread of the disease; who sought to enlist the cooperation of physicians in curing sufferers; and who by means of lectures, demonstrations, and personal conferences tried to convey to the people the importance of being cured, and of putting a stop to soil pollution.

As over-all scientific secretary, Stiles prepared the public as rapidly as possible for the visits of the sanitary inspectors by giving technical and popular addresses to professional and lay audiences, respectively—a total of no less than 246 lectures over the South during the first year.

Areas of infection were first located by the State Director going into sus-

mission
ent to
of the
Page
more
hook-
thing
man-
Free
result.
reach
friend
k was
who
t this
1909.
mmis-
cluded
es as

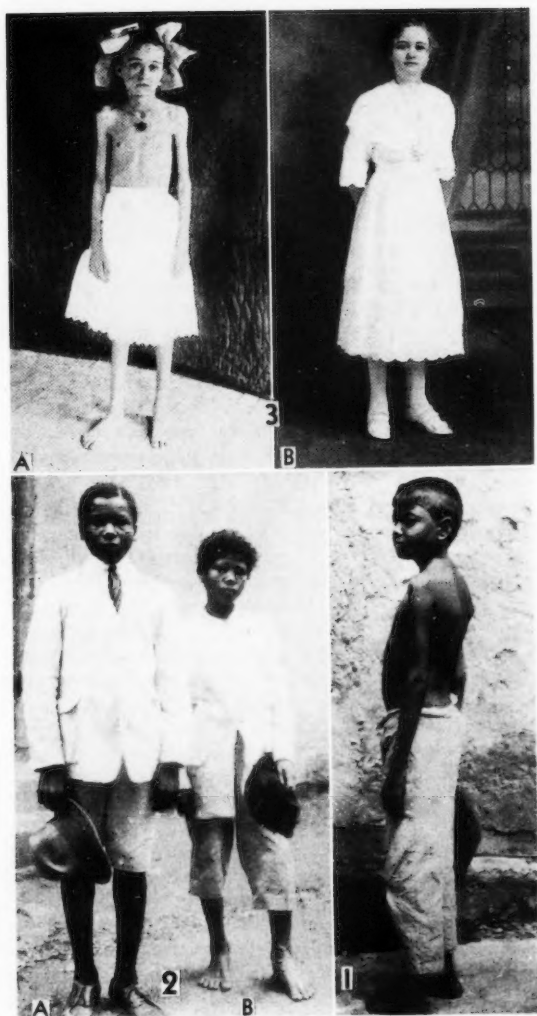
N

nit of
health,
schools
these
popula-
state
body
on as
r nine
nitary

deter-
condi-
ght to
uns of
e peo-
a.

ally as
popular
o less

o sus-



Figs. 1, 3.—1. Case of hookworm infection showing muscular atrophy of shoulders called "angel-wings." 2. Cousins of about the same age. A. Free from hookworms; B. heavily infected, showing severe case of "ground itch" on foot, and stunted growth. (Courtesy Dr. G. C. Payne) 3. A. Sixteen-year-old girl, practically an invalid from childhood; had been treated for malaria and tuberculosis; found heavily infected with hookworms; treated. B. Same girl three years later. (From 4th Ann. Rept., Rockefeller San. Com. Erad. Hookw. Dis.)

pected regions, conferring with local doctors, inspecting a few schools and looking for symptoms in the people along the roads, in country churches, at railroad stations, and at market places in smaller towns. These clinical diagnoses were checked by some microscopic examinations. Over such an area a sanitary inspector was placed to take up the work in detail.

Evidence of the presence of hookworms soon confirmed the early findings of Stiles. Laboratory examination of college students and of state militia showed nearly 40 percent infected; children in an orphanage, 54 percent; and pupils in public schools examined, 82 percent.

The basic objectives of the first year were found to be sound; namely, determining the distribution and degree of infection, getting the people treated, and removing the cause of infection by putting a stop to soil pollution. The cost of treating the indigent was paid by the Commission.

In June of the third year John A. Ferrell, M.D., who had cooperated very actively in the hookworm eradication work in North Carolina, joined the Commission. He had found that "many ills that have been attributed to mental and moral weakness of whole bodies of people are now definitely known to be due to this infection, and curable with its cure." (Fig. 3).

In combating hookworm disease Ferrell had found that the rural school was the greatest medium for the spread of the disease. The infection at times was 100 percent, with all the pupils and the teacher as well victims of the disease. Playing on polluted soil on damp days was found to bring on ground itch. "In this way," Ferrell (1914) wrote, "the pupils at school become infected with the school as an exchange. In a comparatively short time the premises around the homes of all the school children are polluted, and we have the change which anemia produces coming over the community. Progress of the children in school is retarded; the daily attendance is poor; the health of the community is below normal; the crops are not so well cultivated; there is a general backward tendency. The houses are not so well provided for or kept; the whole community is sick and doesn't know it; the economic loss is tremendous."

Conditions Ferrell found in Virginia were characteristic of regions in all the states participating in the drive to eradicate hookworm disease.

By the fourth year of the Commission's work much was being accomplished. The various field units were cooperating with the State laboratories in locating the positive cases, the dispensaries with competent physicians were administering treatments, and local doctors now recognized the disease. This smooth-working cooperation left Stiles free to turn more of his attention to the sanitary work. Cooperation was obtained with the U.S. Department of Agriculture to prepare illustrations and specifications for various models of sanitary units and to distribute them widespread as Farmers' Bulletins. This sanitary work was of such great significance in the prevention of hookworm disease, and Stiles characteristically attacked the problem with such resourcefulness and vigor, that his zoology associates at a banquet in Washington presented him with a wreath and crowned him "a privy counsellor."

The year 1914 was the fifth and last one of the Commission's campaign for the eradication of hookworm disease. As a climax there was a six-weeks county dispensary campaign in various parts of the South. It was intended as a rallying point to which people could be brought to hear lectures, see exhibits of hookworms and photographs, and follow step by step the program which had been developed to locate, treat, and prevent hookworm disease in the future. In the five-year period over 1,000,000 persons were examined, nearly half were found to be infected, and most of these were treated and cured. (Rockefeller San. Com., 1915).

The effective cooperation of the Commission, the practicing physicians, and the state boards of health led to a permanent program that would control not only hookworm disease, but many other serious maladies. The people had been helped to help themselves, and the first public health program had been evolved. Developments of this type later led to the establishment, for the first time, of a county health service with a full-time health officer. In the five-year period appropriations for state health aid increased 81 percent.

AMERICAN HOOKWORM LEADS TO FORMATION OF THE ROCKEFELLER FOUNDATION AND THE INTERNATIONAL HEALTH BOARD

These successes in locating infections, treating patients, and restoring them to health and usefulness were so gratifying that the Commission, in cooperation with the U.S. Public Health Service, began a world-wide inquiry upon the occurrence and distribution of hookworm disease. Infections were reported by 54 counties. In 46 of these, the infection was general and widespread. The area which comprised about 14 million square miles had approximately one billion people living where hookworms were prevalent.

The idea of aiding foreign peoples in reducing the hookworm infections and strengthening the labors of the peoples impressed the ever alert Gates as being an attractive future project. Whereupon, he suggested to Rockefeller the formation of the Rockefeller Foundation, with the International Health Board as one of its divisions (Stiles, 1939). The idea met with ready approval and on May 14, 1913, the Rockefeller Foundation was chartered for, "The well-being of mankind throughout the world." Rockefeller, the president, endowed it with 100 million dollars.

In accordance also with Gates' suggestion, the International Health Commission (Board)⁵ was formed as a division of the Foundation. It received its charter on June 27, 1913, is maintained by funds from the Foundation; and has as its object the "promotion of public sanitation and the spread of knowledge of scientific medicine, with the world as its field." (International Health Commission, 1915).

Proceeding at once to initiate a portion of the world program, Rose, who was made Director-General of the new Board, went to London where in conference with Page, then U.S. Ambassador to England, and with leading

⁵ The name of the International Health Commission was changed to the International Health Board in 1917, and to the International Health Division in 1927.

English medical scientists and Cabinet members they quickly worked out projects for hookworm control in the British Empire (Hendrick, 1924).

Before initiating the foreign work, the International Health Commission made it clear that it would not attempt to eradicate hookworm disease in any foreign country. Such accomplishments would require the operation of permanent agencies working for long periods of time. Rather, the Commission would set a pattern for curing and preventing the disease in selected areas at little cost to the country, with the idea of withdrawing when local agencies had become established.

Pursuant to opening the work in the British tropics, Rose, on a trip late in 1913, made plans for beginning the services in the West Indies. Within four years, the International Health Board had made arrangements for hookworm control work in British Guiana, Trinidad,⁶ Central America, Brazil, China, the Malay States, New Guinea, and Australia; and had added a tuberculosis project in France, a yellow fever program in Venezuela, and malaria work in Southern United States.

Where were the personnel to execute the new public health programs to be found? As yet they were not even trained! A combination of medical and public health training was agreed upon as imperative. Accordingly, the International Health Board, in 1916, asked Johns Hopkins University to assume responsibility for establishing a School of Hygiene and Public Health for which the Board would supply funds for buildings, equipment, and annual maintenance. Not only was a teaching program provided, but a research one as well; and with it the founding of a new scientific periodical, *The American Journal of Hygiene*, to record the results of the researches.

On the heels of the establishment of the new School, other institutions in this and other countries sought similar public health units from various philanthropic sources. Within a decade schools for training public health personnel were established in several states and in South America and Europe.

The accomplishments of these trainees in cooperation with local health units have been reflected in the greatly improved health, the higher standard of living and the increased longevity of the people.

CHINA MEDICAL BOARD FORMED

Also influenced by the American hookworm was the formation of the China Medical Board whose aim was to "promote the gradual and orderly development of a comprehensive and efficient system of medicine in China." In the world survey on the occurrence of hookworm, China was among the countries found to have wide-spread hookworm disease (Rockefeller San. Com., 1911). These blood-sucking worms and other disease-producing organ-

⁶ It was in Trinidad that the writer saw the work of the International Health Board in action, under the direction of Dr. George C. Payne, of the Board, who was adapting the Public Health Program developed by the Rockefeller Sanitary Commission to the field conditions in Trinidad. Dr. Payne and Mrs. Payne collaborated with Dr. W. W. Cort, D. L. Augustine and the writer in investigating sources of human hookworm infections in Trinidad in 1921.

ed out

mission
in any
of per-
mission
areas at
agencies

late in
n four
hookworm
na, the
culosis
ork in

to be
al and
Inter-
ssume
ch for
annual
search
Ameri-

ons in
philan-
sonnel

health
standard

of the
orderly
nina."
g the
San.
organ-

Board
apting
e field
Cort,
ons in



Fig. 4.—Chinese cases of heavily intestinal fluke (*Fasciolopsis buski*) infections. A. Showing characteristic edema. B. Patient showing abdominal edema and a dozen "witch doctor" treatments consisting of blister burns and lymph withdrawals. (Courtesy Dr. C. H. Barlow).

isms greatly limited effective labors of much of the Chinese population because of the extreme shortage of scientifically trained doctors. It was common-place for Chinese patients with abdominal edema due to intestinal worms to appear at the Mission Hospital of Dr. C. H. Barlow with numerous skin burns and blisters inflicted by "witch doctors" to "cure" the patients! (Fig. 4).

Although Christian Missionary Societies had rendered much good medical service, the great need of hundreds of millions in vast areas of China for relief from hookworm and other disease and from "medical" witchery led the China Medical Board in 1915 to purchase from The London Missionary Society the Union Medical College in Peking (China Med. Bd. 1916). With the old Medical College in hand, what was to be done with it? Two main steps were taken: first, to send the most promising Chinese medical men to the United States or to England on ample three-year fellowships for medical training; and second, to employ an American architect to come to Peking and prepare plans and specifications for a modern medical plant. The fellowships which numbered up to 65 in 1918 and cost 50 thousand dollars were of inestimable value not only in the field of medicine but in that of international relations. (China Med. Bd. 1920).

Plans drawn by the architect called for a number of medical buildings which, with their attractive green roofs and scarlet columns, were in harmony exteriorly with the best traditions in Chinese architecture, while their interiors would embody all of the approved features of a modern American medical center. Completed in 1921, the 59 buildings, which included residences for faculty and an electric plant, represented a modern architectural and sanitary engineering project.

In the reorganization period, 1915-1921, the College had grown from a few instructors, students and attendants to a combined group of over 600 workers in the field of scientific medicine. Although the China Medical Board contributed over 44 million dollars to this project, the graduates of the Peiping Union Medical College, as it is now called, are serving the population on both sides of the present struggle. The Chinese civilians have been markedly benefitted physically and spiritually by the philanthropic work of the Board. (Fosdick, 1948).

Worthy of mention as an influence of the American hookworm was the program of domestic and foreign fellowships arranged by Rose of the International Health Division as the Board was now called. The younger gifted men were the ones sought, especially in fields of the natural sciences including preventive medicine. In a period of nine years over 500 young men were chosen from 35 countries for advanced study and international acquaintances. (Gray, 1941).

Of the same general pattern was a project of traveling professors in agriculture and rural life. The first appointee, the Danish attaché who had been a teacher of agriculture in Denmark, visited the boys' and girls' clubs of the Southern United States. Similar clubs were established in Denmark and

nearby countries with the usual valuable results. In excess of 250 persons from 31 nations were enabled by this fellowship project to travel abroad, receiving and disseminating information in their associations with other workers. The Secretary to the King of Iraq, in 1930, was among a group of foreign fellows studying in the United States.

These fellowship projects recall the words of the great English benefactor, Cecil Rhodes, in his last will, "Educational relations make the strongest tie."

HOOKEWORM INFLUENCES DEVELOPMENT OF AGRICULTURAL EXTENSION ACT

In conclusion, the American hookworm also influenced the development and passage of the great Agricultural Extension Act (Smith-Lever Bill) of 1914. Of two of the most effective rehabilitation agencies in the Southern states prior to the passage of the Act, one was "The Farmers' Cooperative Demonstration Work"; the other, the "Rockefeller Sanitary Commission for the Eradication of Hookworm Disease." The former was headed by Dr. Seaman A. Knapp, early southern agriculturalist and exponent of the demonstration farm. His plan for crop culture came into fruition after the Mexican cotton boll weevil had destroyed two consecutive cotton crops, practically bankrupting that section of the country, especially Texas.

Immediate appeals to Congress for aid finally yielded 250 thousand dollars, only half the amount requested to meet the ravages of the weevil (Galloway, 1911). Knapp, who was placed in charge of the project called "The Farmers' Cooperative Demonstration Work," quickly put into operation his plan of deep plowing and early planting of quick-maturing varieties, which demonstrated that cotton could be raised in the South in spite of the boll weevil. But to obtain adoption of this plan throughout the cotton belt was a vast problem. However, the results were so promising that agencies other than Congress contributed. Nominal sums were given annually by the General Education Board until 1908, when Page on learning of the dire effects of hookworm on the Southern population, prevailed upon his friend, Secretary Buttrick of the Board, to increase its contribution to the Demonstration work. The response was immediate. The bequests increased annually until 1914 when 252 thousand dollars were given to increase the numbers of demonstration agents. (Gen. Educ. Bd. 1915).

The great value of being able to grow cotton in spite of the weevil and to improve agricultural productivity generally through the leadership of demonstration agents was rapidly recognized by state after state. By 1910, the improved farming methods and the increased financial support to improve the dire health condition, shown to be due in large part to hookworm infection, combined in effecting ready expansion of the demonstration agents. According to True (1928), there were 450 agents in 12 Southern states in 1910.

Stiles, lecturing in the South where state health programs for hookworm control were being instituted, heard rural people say, "Give us hookworm in-

spectors who know more about agriculture."⁷ Demonstration agents reciprocated in aiding the program of hookworm eradication by stressing the importance of the sanitary phase.

In the midst of this great work Knapp died. Soon friction arose between the Land Grant Colleges and the Federal Department of Agriculture. As a result, the Executive Committee of the Land Grant College Association, and Congressman Asbury F. Lever of South Carolina and Hoke Smith of Georgia (both from hookworm states) conferred on a bill to perpetuate the program of the Farmers' Cooperative Demonstration Work. Such a bill was perfected and introduced into the House by Representative Lever, who fathered the Bill, and into the Senate by Smith. Among the arguments presented for the bill, were: "the agricultural interests as represented by farmers, the colleges, the experiment stations, the agricultural press, and other interests as represented in bankers' associations and *philanthropic agencies of various names* (italics mine), are all united in a desire to see the bill for agricultural extension become a law." (True, 1928).

The Act as passed by Congress in 1914 was hailed by Secretary David F. Houston as the greatest agricultural act ever passed, since it provided for resident county agents in all states to aid in applying new principles and practices to agriculture, for home demonstration agents to bring to the rural homes effective practices in homemaking and for state club leaders to aid in guiding the boys' and girls' agricultural and home project clubs.

Scientific training in agriculture and related fields was markedly stimulated by the passage of the act and the number of graduates soon doubled. Investigators freed from much of the itinerant extension work concentrated upon their researches which increased greatly and proved highly beneficial to agricultural production.

A surprising development was the effect on farm bureaus. The Act, in calling upon these bureaus to aid in raising the county's share of the agent's salary, strengthened the bureaus (Kile, 1921). The resulting cooperation led eventually to the formation of the American Farm Bureau Federation from whose influence farm products began to bring more equitable prices—a major factor in the prosperity of the country.

Under the Extension Act there has been marked development of the boys' and girls' clubs. From 95 thousand members in 1913 (True, 1928), the enrollment increased to nearly two million in 1950. Few sights are more gratifying than the annual gatherings on Land Grant College campuses of thousands of 4-H club youths and their leaders participating in cultural activities and preparing for Christopher Morley's elements of the good life: "learning, earning and yearning."

SUMMARY

Evidence is presented above to show that the announcement of the presence of hookworm in the United States in 1902 by Dr. Charles W. Stiles led to

⁷ Oral statement made by Dr. Charles W. Stiles in Washington, D. C., in 1921.

many constructive developments. Following the discovery, individuals, organizations, cooperating provinces, and countries were led to put forth efforts to control hookworm and many other disease-producing organisms.

The principal organizations that developed from influences of the American hookworm, as here considered, were the Rockefeller Sanitary Commission for the Eradication of Hookworm Disease, the Rockefeller Foundation, the International Health Board, the China Medical Board, the Johns Hopkins School of Hygiene and Public Health and the Peiping Union Medical College.

Some of the accomplishments of these organizations were development of the first public health program, establishment of the county health doctor, education of personnel to execute public health programs, the spread of scientific medicine in China, and cooperation with countries of all the continents in treating groups of the ill and returning them to health and usefulness.

Evidence is presented also to show that the American hookworm in the South influenced the development and passage of the national Agricultural Extension Act of 1914. This Act has resulted in transforming the social life of rural youth, in increasing the volume and value of farm products and in improving the living standard and well-being of millions of Americans.

REFERENCES

- CHINA MEDICAL BOARD, ROCKEFELLER FOUNDATION 1916—First annual report, December 11, 1914-December 31, 1915, 24 pp.
- 1920—Fifth annual report, January 1, 1919-December 31, 1919. New York. 91 pp.
- FERRELL, JOHN A. 1914—The rural school and hookworm disease. U. S. Bur. Educ. Bul. 20. 41 pp.
- FOSDICK, RAYMOND B. 1948—The Rockefeller Foundation, a review for 1947. 64 pp.
- FOSTER, A. O. AND J. W. LANDSBERG 1934—The nature and cause of hookworm anemia. *Amer. Jour. Hyg.* 20(2): 259-290.
- GALLOWAY, BEVERLY T. 1911—Seaman Asahel Knap. Yearbook, U. S. Dept. of Agr. GENERAL EDUCATION BOARD 1915—An account of its activities. New York. 240 pp.
- GRAY, GEORGE W. 1941—Education on an international scale. Harcourt, Brace and Company. New York. 107 pp.
- HENDRICK, BURTON J. 1924—The life and letters of Waler H. Page. Vol. 1. Doubleday, Page. 436 p.
- INTERNATIONAL HEALTH COMMISSION, ROCKEFELLER FOUNDATION 1915—First annual report, June 27, 1913-December 31, 1914. New York. 98 pp.
- KILE, ORVILLE M. 1921—The farm bureau movement. The Macmillan Co. New York. 279 pp.
- ROCKEFELLER SANITARY COMMISSION 1911—Hookworm infection in foreign countries. Pub. 6, Rockefeller San. Com. Erad. Hookworm Dis. 87 pp.
- 1915—Fifth annual report 1914. Pub. 9, Rockefeller San. Com. Erad. Hookworm Dis. 130 pp.
- STILES, C. W. 1902—Hookworm disease in the south. Pub. Health Dept., U. S. Pub. Health & Mar.Hosp. Serv., Wash. Vol. 17, pt. 2 (43): 2433-2534.

- 1909—The importance of preventing soil pollution in order to decrease typhoid fever, hookworm disease, and Cochin-China diarrhea. S. Car. State Bd. Health, Columbia. 12 pp.
- 1910—Hookworm disease, its nature, treatment and prevention. Treas. Dept., Pub. Health and Mar.-Hosp. Serv. U. S., Pub. Health Bul. 32. 40 pp.
- 1939—Early history, in part esoteric, of the hookworm (uncinariasis) campaign in our Southern United States. Jour. Parasit. 25(4): 283-308.
- TRUE, ALFRED C. 1928—A history of agricultural extension work in the U. S., 1785-1923. U.S.D.A., Miscellan. Pub. 15. 220 pp.
- WELLS, HERBERT S. 1931—Observations on the blood sucking activities of the hookworm, *Ancylostoma caninum*. Jour. Parasit. 17(4): 167-182.

The Phloem of *Heterangium americanum*

John W. Hall

University of Minnesota, Minneapolis

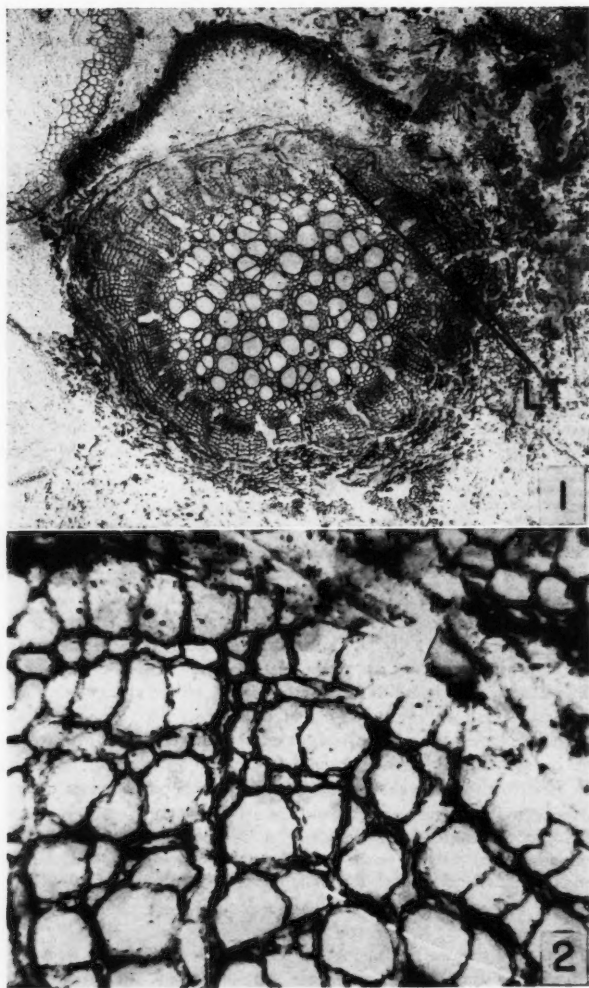
Well preserved phloem in Pennsylvania coal balls is not common. Among the pteridosperms, this tissue has been described mainly from European specimens of *Lyginopteris*, *Medullosa*, and certain species of *Heterangium*. In the latter genus the phloem has been described in some specimens of *H. tiliacoides*; it is less well known in other species (Williamson & Scott, 1896; Renault, 1896; Scott, 1917). As yet, no American specimens of *Heterangium* with phloem structure have been recorded. Based on one well preserved stem of *H. americanum* a contribution can now be made concerning the phloem structure of this American species.

The coal ball containing this stem is from a creek bed near St. Wendells, Posey County, Indiana, which is probably in the upper part of the McLeansboro formation and of Upper Pennsylvanian age; if so it corresponds in stratigraphic position with other specimens of *H. americanum* described by Andrews (1942).

The preserved portion of the stem is an internodal segment measuring approximately 4 cm. in length and 6.5 mm. in diameter; the diameter of the stele, including the secondary tissues, is 4.5 to 5 mm., the difference in width being due to the slightly eccentric production of the secondary tissues. Fig. 1 is a typical cross section of the stem. The very large metaxylem tracheids of the protosteles average 265μ in diameter and are embedded in stellar parenchyma; the protoxylem, with its much smaller spiral and annular tracheids, is eccentrically mesarch (fig. 3). The secondary xylem, composed of circular bordered pitted tracheids, abuts on the periphery of the metaxylem. Between the secondary xylem and secondary phloem is a cambial zone of thin walled cells which are somewhat crushed except in certain regions of the stem. The segment of secondary xylem on the left in fig. 3 shows a few secondary tracheids next to the cambial zone whose radial walls have broken down; these may have been newly formed tracheids whose secondary walls had not been completely lignified before preservation. Multiseriate rays divide the secondary vascular tissues into discrete patches; in the phloem these rays flare out at their distal ends as in *H. tiliacoides*, which *H. americanum* resembles.

A pair of leaf traces approximately 1 mm. apart, each already once divided, can be observed leaving the central cylinder. They move out very gradually, and do not depart from the main axis in the entire length of stem observed. Poorly preserved traces of lower leaves were observed outside the stem, but their course could not be followed, nor were the petioles of any of the lower leaves found associated with this stem.

A zone of thin walled cells, comparable to the pericycle of *H. tiliacoides*, is located to the outside of the phloem; its cells are somewhat crushed. Although not well preserved, this tissue appears to have no trace of the sclerotic



Figs. 1-2.—1. Cross section of stem of *H. americanum*. Above, a portion of the outer cortex has pulled away from the rest of the stem. Also shown are the inner cortex, pericycle, and tissues of the stele. LT, leaf traces. $\times 115$. 2. Cross section of a portion of the phloem and pericycle. Phloem parenchyma cells are in tangential bands, and phloem rays run radially. $\times 185$. Both figures from CB 57a(2).

nests found in the pericycle of *H. tiliaeoides*; secretory or mucilage cells are abundant, however. An inner cortex is indistinctly delimited from the pericycle, with cells somewhat smaller in size than those of the latter tissue. An outer cortex containing sclerotic plates separating broken-down groups of thinner-walled parenchyma cells is the outermost tissue of the stem in one region, where it has pulled away from the inner cortex (fig. 1).

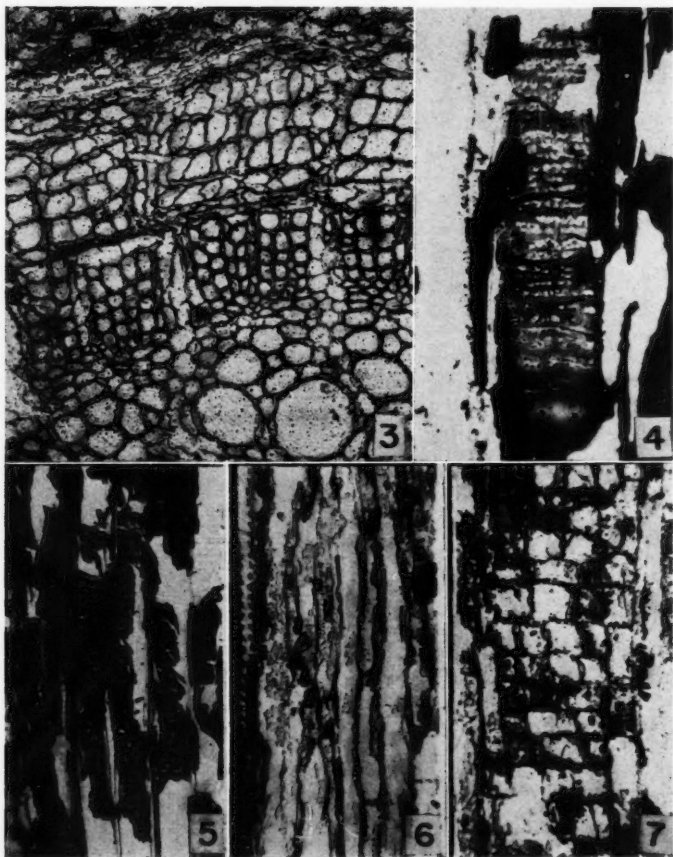
Structure of the Phloem.—The primary phloem is generally badly crushed; it has been observed as a group of small cells at the periphery of some of the segments of secondary phloem. Usually it is forced against the flared ends of the multiseriate rays which cap the phloem masses, in which case its cells are almost indistinguishable from those of the rays.

In this specimen the amount of secondary phloem may equal or exceed the amount of secondary xylem. The width of the secondary phloem ranges from 275μ to 435μ , that of the secondary xylem from 180μ to 470μ .

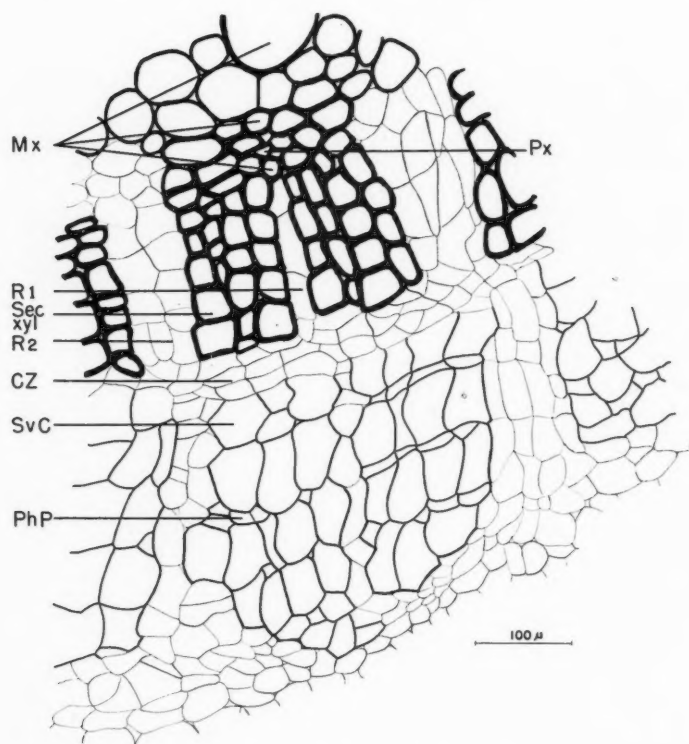
Three types of cells can be recognized in the secondary phloem: sieve cells, phloem parenchyma cells, and cells of the vascular rays (figs. 2, 3). In cross section the sieve cells are mostly square or rectangular, if allowance is made for crushing; many have rounded corners, probably because of mutual pressure before or during preservation. They are arranged in radial rows. The average tangential diameter of the better preserved cells is 44μ .

The two ends of a single sieve cells have not been observed in longitudinal section so that measurements of the actual length of the sieve cells cannot be given. They are undoubtedly very long, however. An indication of their length can be obtained by comparison with the length of the secondary tracheids, which were produced by the same fusiform initials and might be expected to have better preserved ends. Very long tracheids have been found in *Lyginopteris* (5.8 mm.) and *Medullosa* (*M. anglica* 17.5 mm.; *M. Noei* 24.0 mm.) by Andrews (1940), but he gives no figures for the length of the tracheids in *Heterangium*. In the present specimen of *H. americanum*, longitudinal sections 9 mm. long included one end of some, but not both ends of any tracheids, apparently indicating that the tracheids are as long as those in *Lyginopteris*, if not longer. That the sieve cells are correspondingly as long may reasonably be assumed; in fact, some of the sieve cells can be followed for almost the entire length of the sections without finding end walls. Where one end has been observed it is always the blunt end of typical sieve cells.

The lowermost 2-3 mm. of the stem appears to have been charred; the cells in this region are highly carbonized. It is principally here that the sieve plates are well preserved. The sieve areas are numerous but not crowded, and are confined to the radial walls of the sieve cells. They vary in shape from lenticular to almost circular and bear many pores (figs. 4, 5). They appear to resemble those of modern cycads, such as *Microcycas*. Williamson and Scott (1896) have suggested that the preservation of fine detail in the sieve plates of *H. tiliaeoides* is due to carbonization of the contents of the sieve tubes and their adherence to the sieve plates as a thin carbonaceous print. This explanation may apply to this specimen of *H. americanum* as well. There appears to



Figs. 3-7.—3. More highly magnified portion of stem shown in fig. 1. The tissue beyond the phloem rays is the pericycle. $\times 125$. 4. Portion of a sieve cell with sieve plates on radial wall. $\times 460$. 5. Radial section of sieve cells with numerous sieve plates. $\times 150$. 6. Radial section of phloem showing two complete cells of a strand of phloem parenchyma. $\times 150$. 7. Portion of phloem ray in radial section. Nucleus-like structures are visible in some of the ray cells. $\times 135$. Fig. 3 from CB 57a(2), all others from CB 57b(2).



Camera lucida drawing of a segment of xylem and phloem. Px, protoxylem; Mx, metaxylem; R 1, uniseriate ray; Sec Xyl, secondary xylem; R 2, multiseriate ray; CZ, cambial zone; SvC, sieve cell; PhP, phloem parenchyma cell. From CB 57a(2).

have been a coagulation of the protoplasmic contents of the living cells in the carbonized portion of the stem and in a region extending some 3.4 mm. from it. Many phloem ray cells in this entire region are filled with a blackish-brown residue which may have been protoplasm, and many of the cells bear a single spherical object of the size and spatial relationships of a nucleus (fig. 7). In the less carbonized regions the phloem ray cells are empty.

Small phloem parenchyma cells occur in alternating tangential bands with the sieve cells. In cross section the parenchyma cells sometimes occur in rows of 3 to 10 cells extending tangentially in the phloem segments between two multiseriate rays, but may be isolated or in clusters of 2 or 3 among the

sieve cells. They are apparently easily obliterated, since they do not seem to be as abundant in the less well preserved portions of the phloem. In longitudinal section they occur as strands two or more cells long. The longest strand was 11 cells, in tangential section, but most are not longer than 5 cells (fig. 6). The parenchyma cells range in length from 35μ to 135μ and average 63μ ; their width in radial section averages 20μ .

The uniseriate rays of the secondary phloem are quite tall. In radial section they range up to 60 cells or more (3 mm.). Their constituent cells are parenchymatous and mostly isodiametric; many bear what appears to be a nucleus (fig. 7).

The phloem of *H. americanum* is quite similar to the phloem of some present day cycads. For instance, the first formed secondary phloem of *Microcycas calocoma*, which Chrysler (1926) has studied, exhibits in a modern cycad many of the features of the phloem anatomy of *H. americanum*. In *Microcycas* there are two zones of secondary phloem. The first formed contains sieve cells and parenchyma cells only; in the second zone fibers are found in addition to the sieve cells and phloem parenchyma. As Chrysler has pointed out, there is a great similarity in the structure of the first formed phloem of *Microcycas* and that of certain pteridosperms. The phloem of *H. americanum* again bears out his observation. The same types of cells are found in both *Heterangium* and *Microcycas*, except, of course, that there are fibers in the second formed phloem zone of *Microcycas*. The markings on the sieve cells and the arrangement of phloem parenchyma cells are similar in both genera. Although additional examples of the phloem of pteridosperms would be desirable for critical comparisons, attention can be drawn to the underlying similarities in structure between the secondary phloem of the pteridosperms and the cycads.

ACKNOWLEDGMENTS

Appreciation is expressed to the Illinois State Geological Survey for the loan of the material in which this specimen was found. The author also wishes to acknowledge the aid given by Professor Wilson N. Stewart in the preparation of this paper.

REFERENCES

- ANDREWS, H. N. 1940—On the stelar anatomy of the Pteridosperms with particular reference to the secondary wood. *Ann. Mo. Bot. Gard.* 27: 51-118.
——— 1942—Contributions to our knowledge of American Carboniferous floras. V. *Heterangium*. *Ibid.* 29: 275-282.
CHRYSLER, M. A. 1926—Vascular tissues of *Microcycas calocoma*. *Bot. Gaz.* 82: 233-252.
RENAULT, B. 1896—Bassin houiller et permien d'Autun et d'Epinaç. *Flore Fossile. Étude des Gites Minéraux de la France.*
SCOTT, D. H. 1917—The *Heterangium*s of the British coal measures. *Jour. Linn. Soc. Bot.* 44: 59-105.
WILLIAMSON, W. C. AND D. H. SCOTT 1896—Further observations on the organization of the fossil plants of the coal-measures. Part III. *Lyginodendron* and *Heterangium*. *Phil. Trans. Roy. Soc. Lond.* 186(B): 703-779.

7 (3)

m to
ongi-
ngest
cells
and

sec-
s are
be a

some
n of
mod-
ium.
rined
s are
ysler
rmed
f H.
s are
e are
n the
ur in
erms
the
the

of the
ge the

icular

Y.
233-

ossible.

Soc.

ization
eter-

REPRINT SERIES

(Reprints 1, 2, 3 were issued with volume 2, reprint
4 with volume 3 and reprint 5 with volume 5).

(1) RAFINESQUE, C. S.—Neogenyton. 1825.....	\$.25
(2) ———The Natural Family of Carexides. 1840.....	.50
(3) ———Scadiography of 100 Genera of Umbelliferous Plants, etc. 1840	1.50
(4) ———Monographie des Coquilles Bivalves et Fluviatiles de la Riviere Ohio. Remarques sur les Rapports Naturels des Genres Viscum, Samolus et Viburnum. A Bruxelles. 1820	1.50
(5) LeCONTE, J. E.—Reprints of Monographs without plates.....	2.50
With 42 photographic copies of unpublished plates (7 × 8).Prices on request	
—Two extra plates reproduced from originals in New York Botanical Garden	Prices on request

PUBLICATIONS

AMMONS, NELLE.—A Manual of the Liverworts of West Virginia, 1940. Cloth	\$ 1.75
BAILEY, V.—Cave Life of Kentucky. 1933.....	1.25
BARKLEY, FRED A.—Keys to the Phyla of Organisms Including Keys to the Orders of the Plant Kingdom. 1939. 44 pp., paper bound.50
CARPENTER, MATHILDE M.—Bibliography of Biographies of Entomolo- gists. 1945. 116 pp.....	.75
GREENE, E. L.—Manual of the Botany of the Region of San Francisco Bay. 1894. Bound cloth.....	2.00
Unbound	1.50
—Flora Franciscana. Part 2. 1895.....	.75
—Plantae Bakerianae. 1-3.....	1.30
—Cybele Columbiana. A Series of Studies in Botany, chiefly North North American. (All published). 1914.....	.75
SEVERAL AUTHORS—Plant and Animal Communities. 1939. Cloth.....	2.50
KISTLER, ELLEN D.—Bibliography of the Botanical Writings of Edward Lee Greene. 1936.....	.25
SCHUSTER, R. M.—The Ecology and Distribution of Hepaticae in Cen- tral and Western New York. 1950. Cloth.....	2.50
SETTY, L. R. AND KENNETH W. COOPER—Studies in the Mecoptera. 1940	1.00
TOWNES, HENRY K., JR.—The Nearctic Species of Tendipedini [Dip- tera, Tendipedidae (=Chironomidae)]. 1945	1.00
WOLFENBARGER, D. O.—Dispersion of Small Organisms. 1946	1.00

THE AMERICAN MIDLAND NATURALIST

Monograph Series

- No. 1. The Argasidae of North America, Central America, and Cuba.
By R. A. Cooley and Glen M. Kohls. 1944. Cloth, \$2.00.
- No. 3. The Mosquitoes of the Southern United States East of Oklahoma and Texas
By Stanley J. Carpenter, Woodrow M. Middlekauff and Roy W. Chamberlain. 1946. Cloth, \$4.00.
- No. 4. Woody Plants of the Western National Parks.
By Virginia Long Bailey and Harold Edwards Bailey. 1949. Cloth, \$4.00.
- No. 5. Flora of Illinois.
By George Neville Jones. 1950. Cloth, \$4.25.
- No. 6. A Manual of the Mosses of Western Pennsylvania and Adjacent Regions. Second Edition.
By O. E. Jennings. 1951. Cloth, \$4.25.

The American Midland Naturalist Monographs are reserved for large contributions and may be obtained by purchase or on exchange basis.

In the Next Issue

- The Genus *Helianthella*.....William A. Weber
- Carex acutiformis* in Indiana.....F. J. Hermann
- Notes on Wisconsin Parasitic Fungi. XV.....H. C. Greene
- Uniparental Miracidia of *Schistosomatium douthitti* and their progeny (Trematoda, Schistosomatidae).....Robert B. Short
- Two New Species of *Oochoristica* from Minnesota Skunks.....Asa C. Chandler
- Host Relationships and Seasonal Abundance of Some Southwest Georgia Parasites.....Harvey B. Morlan
- The Preputial Organ of Snails in the Genus *Helisoma* (Gastropoda: Pulmonata).....Emile T. Abdel-Malek
- Records and Flower Preferences of Masarid Wasps. II. Polytypy or Oligotypy in *Pseudomasaris*? (Hymenoptera: Vespidae).....Kenneth W. Cooper
- The Ant Larvae of the Subfamily Ponerinae—Part I.....George C. and Jeannette Wheeler
- Additional New Species in the Genera *Anopompilinus*, *Ahoplius*, *Pompilinus*, and *Pycnopompilus* (Hymenoptera: Psammocharidae) and Corrections of Previous Papers.....R. R. Dreisbach
- Types and Figured Specimens of Fossil Fishes in the Patten Collection, Dartmouth College Museum, Hanover, New Hampshire.....Robert H. Denison
- The Relationship of the Chorus Frogs, *Pseudacris nigrita* feriarum and *Pseudacris n. triseriata*.....Philip W. and Dorothy M. Smith
- Evidence for Olfactory Discrimination by the Bobwhite Quail.....Hubert Frings and William A. Boyd
- Columbian Sharp-tailed Grouse (*Pedioecetes phasianellus columbianus*) in the State of Washington.....Charles F. Yocom
- Ecology and Helminths of the Osage Wood Rat, *Neotoma floridana* osagensis, Including the Description of *Longistriata neotoma* n. sp. (Trichostrongylidae).....Melvin F. Murphy
- The Foods of Fur Animals of the Patuxent Research Refuge, Maryland.....Leonard M. Llewellyn and Francis M. Uhler
- Life History Studies of the Water Shrew (*Sorex palustris navigator*).....Clinton H. Conaway
- The Parotid Gland of an Anteater, *Tamandua tetradactyla*.....Walter W. Dalquest and H. J. Werner

a
y
.
t
e

Short
andler

Morlan

Malek

Cooper
heeler

isbach

enison

Smith

Boyd

Yocom

Murphy

Uhler
onaway

Verner